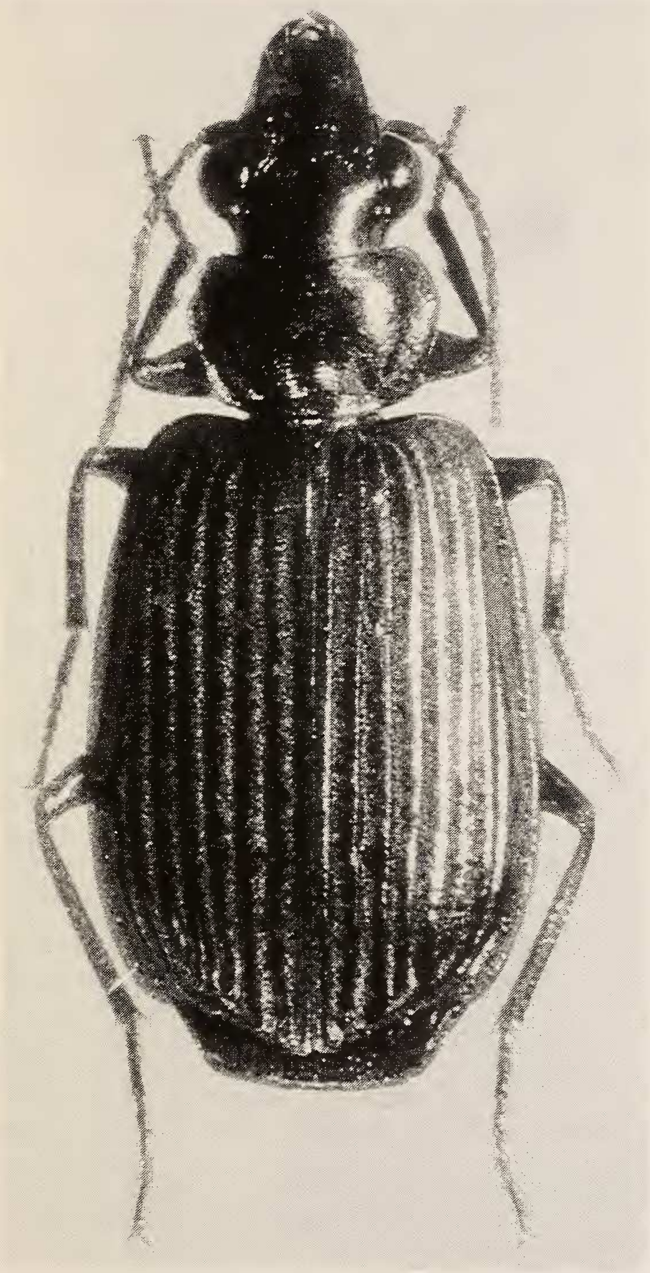

FRONTISPIECE. Photograph of habitus of *Coptodera brunnea*, new species, dorsal aspect. USA, Arizona, Huachuca Mtn., Ash Canyon Road (CNC). SBL = 6.16 mm.

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CLASSIFICATION, RECONSTRUCTED PHYLOGENY AND GEOGRAPHICAL HISTORY OF THE NEW WORLD SPECIES OF *COPTODERA* DEJEAN (COLEOPTERA: CARABIDAE: LEBIINI)

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Abstract *Proc. ent. Soc. Ont.* 124: 3-182

Keys, descriptions, and illustrations distinguish the known New World species of *Coptodera* (type species—*Coptodera festiva* Dejean), and each taxon is characterized in terms of structural features of adults, habitat, geographical distribution, chorological affinities, and phylogenetic relationships. Twelve new species are described.

The New World species of *Coptodera* are arranged in eleven groups, sequenced according to the reconstructed phylogeny: *C. sallei* group, including *C. sallei* new name; *C. elongata* group, including *C. elongata* Putzeys, *C. schaumi* Chaudoir, *C. megalops* Bates, *C. championi* Bates, and *C. apicalis* new species (type locality—Ecuador, Esmeraldas, Zapallo Grande); *C. aurata* group, including *C. xanthopleura* Bates, *C. aurata* Chevrolat, and *C. viridis* new species (type locality—México, Colima, near Ixtapa); *C. depressa* group, including *C. depressa* Dejean and *C. versicolor* Bates; *C. transversa* group, including *C. dromioides* (Bates), *C. nigrosignata* (Chaudoir); *C. fulminans* (Bates), *C. nigrostriata* (Reiche), *C. lineata* (Bates), *C. stockwelli* new species (type locality—Panamá, Canal Zone, Madden Forest), *C. transversa* (Reiche), *C. sigillata* new species (type locality—Brazil, Santa Catarina, Nova Teutonia), and *C. squiresi* (Chaudoir); *C. festiva* group, including *C. sahlbergi* Chaudoir, *C. relucens* Bates, *C. poecila* Bates, *C. pakitza* new species (type locality—Peru, Madre de Dios, Pakitza), *C. festiva* Dejean, *C. foveolata* new species (type locality—México, Veracruz, Tebanca), *C. nigroviridis* new species (type locality—México, Chiapas, Parque Montebello), *C. rufescens* Buquet, and *C. teutonica* new species (type locality—Brazil, Santa Catarina, Nova Teutonia); *C. aeneorufa* group, including *C. aeneorufa* Bates; *C. bifasciata* group, including *C. bifasciata* Putzeys, *C. tripartita* Chaudoir, *C. cupreotincta* Bates, and *C. braziliensis* new species (type locality—Brazil, Santa Catarina, Hansa Humboldt); *C. emarginata* group, including *C. chalcites* Bates, *C. emarginata* Dejean, and *C. acutipennis* (Buquet); *C. picea* group, including *C. picea* Dejean; and *C. aerata* group, including *C. nitidula* (Buquet), *C. brunnea* new species (type locality—United States, Arizona, Cochise County, Guadalupe Canyon), *C. aerata* Dejean, *C. waytkowskii* Liebke, *C. erwini* new species (type locality—Peru, Madre de Dios, Pakitza), and *C. tripunctata* new species (type locality—Peru, Loreto, Cocha Shinguito).

Removed from synonymy with *C. lineata* Chaudoir is *C. nigrosignata* Chaudoir, the name of a valid species.

Ten synonymies are newly proposed with the senior synonym of each combination listed first: *Coptodera* Dejean = *Stenoglossa* Chaudoir; *C. megalops* Bates = *C. pertzeli* Liebke = *C. peruana* Liebke; *C. depressa* Dejean = *C. plaumanni* Liebke; *C. sahlbergi* Chaudoir = *C. discicollis* Chaudoir; *C. festiva* Dejean = *C. chloris* Bates; *C. cupreotincta* Bates = *C. tesselatus* Chaudoir; *C. acutipennis* (Buquet) = *C. scintillans* Bates; *C. picea* Dejean = *C. unicolor* Chevrolat; *C. nitidula* (Buquet) = *C. triangularis* (Buquet) = *C.*

nubiculosa Chaudoir = *C. flavodisca* Chaudoir; *C.lineata* (Bates) = *C. nigrosignata* (Chaudoir); and *C. transversa* (Reiche) = *C. picturata* (Chaudoir) = *C. undulata* (Chaudoir).

One replacement name is proposed for a junior homonym: *C. sallei* for *C. variegata* Chaudoir.

Six species are removed from *Coptodera* and placed into other genera in the following new combinations: *Microlestodes marcida* Blackburn, *Anchista philippinensis* Jedlička, *Stenognathus robustus* Bates, *Lelis polygona* Bates, *Lelis latipennis* Bates, and *Lelis rutila* Bates.

Coptodera fasciolata Macleay is given new status as the previously used name, *C. aurata* Macleay, and synonym, *C. tesselatus* Chaudoir (1883), are both junior homonyms of *C. aurata* Chevrolat and *C. tesselatus* Chaudoir (1869) respectively.

Based on analysis of 136 character states representing 55 morphological characters (including color), the postulated phylogenetic relationships of the New World species groups of *Coptodera* are: (*sallei*- [*elongata* + *aurata*]) - (*depressa*- (*transversa* - (*festiva*- (*aeneorufa* - {[*bifasciata* + *emarginata*] + [*picea* + *aerata*]}))). Postulated phylogenetic relationships of the species of each group are provided in the text. Most sequences are short, each such involving development of an apotypic state followed by stasis or reversal, and without continued specialization of the apotypy. However, postulated convergences and reversals are numerous. This latter aspect of character evolution may be a reflection of the seemingly slight ecological differentiation of the genus (almost all species are associated with loosened bark on living or dead tree trunks), with lineages being subjected to the same kinds of selective forces but in different combinations in different areas and under oscillating climatic regimes.

Evolution of the extant New World species of *Coptodera* is postulated to have taken place in the tropics, during the time period Late Cretaceous-Recent. Both South America and Middle America + U.S.A. have distinct species assemblages, with most of the evolution of the *sallei* - *elongata* - *aurata* complex having occurred in Middle America, and most of the evolution of the *depressa* - *aerata* complex having taken place in South America.

The evolution of *Coptodera* seems to have involved 14 invasions of Middle America from South America, and four reverse invasions, from Middle America to South America. The fewer, earlier invasions are postulated to have involved crossing of seaways that isolated South America from Middle America, with the more numerous later invasions having taken place when the northern and southern continents were joined by the present Panamanian land connection.

Two lineages, represented respectively by *C. festiva* and *C. picea*, reached the West Indies and southern Florida, probably comparatively recently. Three lineages of the *C. aerata* species group invaded the temperate forests of southern United States: *C. brunnea* and *C. nitidula* did so comparatively recently, and only in the southwest. The ancestral stock of *C. aerata*, the only species of *Coptodera* confined to the North Temperate zone, reached the north at an earlier period.

Because of extensive allopatry and near allopatry of closely related species a general coincidence of geographical range limits and areas of endemism or of refugia (recognized previously on the basis of chorological evidence from plant and other animal taxa), the causes of differentiation of *Coptodera* are to be sought in the general context of tropical forest refuge theory, which postulates recurring cycles of range expansion and contraction. Differentiation is associated with periods of generally unfavorable climate, resulting in extinction of the forest biota over extensive areas, with its survival in geographically isolated areas that provide local more favorable environmental conditions (the refugia).

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Introduction

The New World species of *Coptodera* Dejean have not been revised since Chaudoir (1869). However, Bates also published a taxonomic treatment of *Coptodera* in that same year, but earlier than Chaudoir. Since each had duplicate specimens of a number of species, several of Chaudoir's new species names were subsequently synonymized with those described by Bates. Liebke (1939, 1951) was the most recent taxonomist to describe several additional species.

While studying the species of *Celaenephes* Schmidt-Goebel and *Euproctinus* Leng & Mutchler, an interest in *Coptodera* was developed. The species in the *Coptodera aerata* group have sensory pits on the ventral surface of antennomeres 5-11 (Figs. 1A-1B) similar to those seen in *Celaenephes* and Metallicine Lebiini. This interest was the starting point for the revision of the New World species of *Coptodera.*

History of Classification of *Coptodera*

The genus *Coptodera* had been included in the pericaline assemblage (Pericalides [Lacordaire 1854: 137], "*Coptodera* and allies" [Bates 1869], Coptoderides [Chaudoir, 1869], or Catascopi [Csiki, 1932: 1352]) since this group of lebiines first was recognized by Lacordaire. Bates (1869: 69), in his inimitable natural historian's approach, brought meaning to the diagnostic features of the pericaline assemblage by noting that the flattened body form and elongate mouthparts with nearly straight mandibles were of adaptive significance to insects living and hunting beneath rather tight-fitting bark of dead or dying trees.

Jeannel (1949) organized the pericaline assemblage of previous authors into two units: the Thyreopteridae (p. 1006) in which he included *Pericalus* Macleay, and the subfamily Coptoderitae (p. 924) of family Lebiidae. In doing so, he ignored the marked similarity between the two groups.

Most subsequent authors (Jedlička 1963; Habu 1967; Ball 1975; and Ball and Shpeley 1983) did not follow Jeannel, but included the coptoderine assemblage with the thyreopterines. Basilewsky (1984: 538-543), in his thought-provoking classification of the genera of African-Madagascan Lebiinae, accepted Jeannel's bipartite arrangement of the pericaloids, but ranked them as tribes (Mormolycini = Thyreopteridae; and Pericalini = Coptoderinae), which were placed in juxtaposition to one another. Also, he included *Pericalus* and *Coptodera* in the same tribe.

Hansen (1968) followed Jeannel in recognizing a subfamily Coptoderinae, but did not discuss its affinities, nor did he present his concept of the more inclusive lebiine assemblage.

Ball (1975: 176), Ball and Shpeley (1983: 751) and Basilewsky (1984: 542) agreed that *Pericalus* Macleay and *Coptodera* were closely related, and that they must be classified together, based on synapotypic features of mouthparts and ovipositor. Basilewsky, however, ranked the inclusive group as a tribe, and recognized two subtribes: Coptoderina, to include *Coptodera* and its immediate relatives that Jeannel and Hansen placed in the Coptoderinae; and the Pericalina, to include *Pericalus*, only. Ball, and Ball and Shpeley included *Coptodera* (*sensu latissimi*) in the pericaloid assemblage of genera, within the subtribe Pericalina.

At the generic level, Jeannel (1949: 924) included in *Coptodera* only New World species, distributing the Old World species among eight genera, most of which were proposed by him. Hansen (1968) followed Jeannel, and proposed two additional genera.

Material and Methods

Materials

This study is based on examination of 2901 adult *Coptodera*, including types of most species, 26 adult *Pericalus* Macleay and three adult *Somotrichus* Seidlitz. Some of the material was available in the Strickland Museum, University of Alberta (UASM). Additional material was borrowed from, or deposited in, the following institutions and private collections, noted in the text by the associated codens. Names of curators are provided also.

AMNH	Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York, U.S.A. 10024 (L.H. Herman)
BMNH	Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD (N.E. Stork)
CAS	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, U.S.A. 94118 (D.H. Kavanaugh)
CDAE	California State Collection of Arthropods, Department of Food and Agriculture, 1220 N. Street, Sacramento, California, U.S.A. 95814 (F.G. Andrews)
CMNC	Canadian Museum of Nature, Entomology, P.O. Box 3443, Station D, Ottawa, Ontario, Canada K1P 6P4 (R.S. Anderson)
CMNH	Section of Entomology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania, U.S.A. 15213 (R.L. Davidson)
CNC	Canadian National Collection, Biosystematics Research Institute, Agriculture Canada, K.W. Neatby Building, Ottawa, Ontario, Canada K1A 0C6 (Y. Bousquet)
CUIC	Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York, U.S.A. 14850 (J.K. Liebherr)
DAPC	Darren A. Pollock, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada T6G 2E3
DEUN	Division of Entomology, University of Nebraska State Museum, University of Nebraska, Lincoln, Nebraska, U.S.A. 68503 (B.C. Ratcliffe)
DHK	David H. Kavanaugh, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, U.S.A. 94118
EGRC	E.G. Riley, Department of Entomology, Texas A&M University, College Station, Texas, U.S.A.
FMNH	Department of Zoology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois, U.S.A. 60605 (P.P. Parrillo)
FSCA	Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Gainesville, Florida, U.S.A. 32601 (R.E. Woodruff)
GRNC	G.R. Noonan, Insect Collection, Milwaukee City Public Museum, 800 West Wells Street, Milwaukee, Wisconsin, U.S.A. 53233
HECO	Hope Entomological Collections, University Museum, Parks Road, Oxford, England OX1 3PW (S. Simpson)
HFRE	H. Freude, I-60015 Falconara, Via Sadegna 7, Italy
HHES	H.A. Hespenheide, Department of Biology, University of California, Los Angeles, California, U.S.A. 900241606
HNHM	Zoological Department, Hungarian Natural History Museum, H-1088 Budapest, Baros u. 13, Hungary (O. Merkl)
HPST	H.P. Stockwell, from material on loan from USNM (see below)

IVIE	M. Ivie, Department of Entomology, Montana State University, Bozeman, Montana, U.S.A. 59717
IZWP	Instytut Zoologii, Polska Akademia Nauk, 00-679 Warszawa, Poland, ul. Wilcza 64 (S.A. Slipinski)
JAMU	Science Museum, Institute of Jamaica, 12-16 East Street, Kingston, Jamaica (T.H. Farr)
JEWC	J.E. Wappes, RD 2 Box 16BB, Chadds Ford, Pennsylvania, U.S.A. 19317
JMPR	Julio Micheli, 14 Baldorioty St.-Mariani, Ponce, Puerto Rico, U.S.A. 00731
LSUC	Louisiana State University Insect Collection, Department of Entomology, Louisiana State University, Baton Rouge, Louisiana, U.S.A. 70803 (V.L. Moseley)
MCSN	Museo Civico de Storia Naturale "Giacoma Doria", Via Brigita Ligurua 9, I-16121 Genoa, Italy (R. Poggi)
MCZ	Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachussetts, U.S.A. 02138 (S.R. Shaw)
MNHB	Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität zu Berlin, 104 Berlin, Invalidenstrasse, D.D.R. (F. Hieke)
MNHP	Entomologie, Museum National d'Histoire Naturelle, 45 Rue Buffon, Paris, 75005, France (H. Perrin)
MPEG	Departmento de Entomologia, Museu Paraense Emilio Goeldi, C.P. 399, Belem, Para 66000, Brazil.
MPMM	Insect Collection, Milwaukee City Public Museum, 800 West Wells Street, Milwaukee, Wisconsin, U.S.A. 53233 (G.R. Noonan)
MSUC	Department of Entomology, Michigan State University, East Lansing, Michigan, U.S.A. 48823
MZUM	Museum of Zoology, Insect Division, The University of Michigan, Ann Arbor, Michigan, U.S.A. 48109-1079 (M. O'Brien)
MZSP	Museu de Zoologie, Universidade de São Paulo, Caixa Postal 7172, São Paulo, Brazil (C. Costa)
OSUC	Department of Entomology, Ohio State University, 1735 Neil Avenue, Columbus, Ohio, U.S.A. 43210 (C.A. Triplehorn)
QCAZ	Quito Catholic Zoology Museum, Department de Bilogia, Pontificia Universidad Catolica del Ecuador, 12 de Octubre y Carrion, Apto. 2184, Quito, Ecuador
RHTC	Robert H. Turnbow, Directorate of Engineering and Housing, Building 1404, Fort Rucker, Alabama, U.S.A. 36362-5137
RTAC	R.T. Allen, Department of Entomology, University of Arkansas, Fayetteville, Arkansas, U.S.A. 72701
SEMC	Snow Entomological Museum, The University of Kansas, Lawrence, Kansas, U.S.A. 66045-2119 (J.S. Ashe, R. Brooks)
SMC	Scott McCleve, 2210-13 Street, Douglas, Arizona, U.S.A. 85607
SPC	S.B. Peck, Department of Biology, Carleton University, Ottawa, Ontario, Canada K1S 5B6
TAMU	Department of Entomology, Texas A&M University, College Station, Texas, U.S.A. (H.R. Burke)
UADE	Department of Entomology, University of Arkansas, Fayetteville, Arkansas, U.S.A. 72701 (R.T. Allen)
UCBC	Division of Entomology and Parasitology, University of California, Berkeley, Berkeley, California, U.S.A. 94720 (J.A. Chemsak)

UCDC	The Bohart Museum of Entomology, University of California, Davis, California, U.S.A. 95616
UGCG	University of Guatemala Collection, Guatemala City, Guatemala (J. Schuster)
USNM	Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. 20560 (T.L. Erwin)
ZSMM	Zoologische Staatssammlung, Münchhausenstrabe 21, D-8000, München 60, Federal Republic of Germany (G. Scherer)

Methods

Taxonomic concepts, principles, criteria for ranking, and general working methods were the same as those previously described (Ball 1975, 1978; Allen and Ball 1980).

Measurements.-- Measurements were made with an ocular micrometer in a Wild M5 stereoscopic microscope, at 12X, 25X or 50X. Measurements of body parts and abbreviations used for them in text and tables are:

Length of head (Hl) - linear distance from base of left mandible to posterior margin of left compound eye;

Width of head (Hw) - maximum distance across the head, including the compound eyes;

Length of pronotum (Pl) - linear distance from anterior to posterior margin, measured along the midline;

Maximum width of pronotum (Pw) - greatest linear transverse distance;

Length of elytra (El) - linear distance from basal ridge to apex of longer elytron, measured along the suture.

Standardized Body Length (SBL), used as an index of overall size, is the sum of Hl, Pl, and El.

Preparation of material.-- Dissections were made using standard techniques. Genitalia and other small structures were preserved in glycerine in microvials, pinned beneath the specimens from which they were removed. Larger structures and those that were gold-coated for study with the SEM were glued to cards pinned beneath the specimens from which they were removed.

Photographs of isolated structures were taken with a Cambridge S-150 "Stereoscan" Scanning Electron Microscope (SEM).

Line drawings of selected body parts were prepared using a camera lucida on a Wild M5 stereoscopic microscope. The figures of male genitalia with macrospines on the internal sac are illustrated in such a manner as to give a notion of their orientation. When the base of a macrospine is filled in (black), the reader is looking down on the base. When the base of a macrospine is open (white), the reader is looking at the opposite surface of it (this is the attachment area of the macrospine to the internal sac).

Special maps were prepared for species or species groups whose ranges extended from México to South America. The region from the Isthmus of Tehuantepec, México to the Panamá-Colombia border is enlarged to better illustrate the distribution patterns.

Notes about descriptions.-- To avoid repetition, character states of lower-ranking taxa recorded in the descriptions of higher-ranking taxa are not repeated in the descriptions of the included lower-ranking taxa. Thus, the complete description of a species must be assembled from its taxonomic placement. Such a description can be obtained by reading the descriptions and diagnoses of the sequence of higher-ranking taxa in which the lower-ranking taxon is placed.

Supraspecific ranking.-- Clusters of species are evident, based on features postulated to be synapotypic, and on distribution pattern or chorological similarity. To designate these monophyletic clusters, the informal category "species group" is used. Although a single supraspecific-infrageneric level is sufficient to accommodate the New World taxa, a general revision of *Coptodera* (*sensu latissimi*) no doubt will reveal additional levels between genus and species. To accommodate these levels, additional supraspecific ranks, such as subgenus and subgroup will be required.

Catalogue citations of species names.-- Catalogue entries noted in the synonymy of the genus *Coptodera* are not repeated in the species' synonymies: Blackwelder (1944); Csiki (1932); Erwin *et al.* (1977); and Leng (1920).

Label data.-- For type material, the data on each label are reported as exactly as is possible. For other material, only the actual locality and depository of specimens are given. Label data about altitude and date of collection are reported in summary fashion under the headings "Notes about habitat" and "Material examined" respectively.

Terms

Terms for structural features

Most of the words used to designate details of structures are found in textbooks of general entomology, or are used by coleopterists, generally. Other words, required to designate particular structures or parts thereof, are not in general use, though they have been used by us in previous publications. We provide information about these words here.

Microsculpture.-- A "*sculpticell*" is the space enclosed on the surface of the cuticle by adjacent microlines of the integumental system of microsculptue (Allen and Ball 1980: 485-486).

Body parts.-- The term "*segment*" is restricted to those body parts that reflect embryonic somites; thus, somite-like portions of the abdomen are referred to as segments. Abdominal segments are designated by Roman numerals corresponding to the respective somites. The first complete sternum is III, and the last one normally exposed is VII. For numbering the genital somites we follow Bils (1976).

Portions of appendages are designated by the suffix "*-mere*", the prefix depending upon the appendage in question: *antenno-*, *palpo-*, *tarso-*, *et cetera.*

Mandibles.-- Acorn and Ball (1991) summarized previous efforts to describe the features of the mandibles of Carabidae and proposed a modified and more complete system of names. The names offered below reflect this general system, as applied to the mandibles of *Coptodera.*

As in other pericalines (cf. Ball 1975), the mandibles of *Coptodera* adults exhibit reductions and losses, compared to more generalized lebiines and members of most other tribes. Table I lists the diagnostic features of the left and right mandibles for each of the *Coptodera* species groups. The mandibles are trigonal, with broad bases and form falcate (Figs. 2-4). Both mandibles are curved medially, apically. Areas are a broad basal or molar area (m), and the more slender tapered terebra (t), terminated in the acute incisor tooth (i). The dorsal surface of the terebra is strigulose (ts), more or less extensively. The occlusal margin basally is terminated by a group of setae, termed basal brush (bb), Ball's (1975: 149) statement to the contrary notwithstanding. A series of ridges and grooves on the ventral surface is exhibited clearly in occlusal aspect, and best described for left and right mandibles, separately. Ventrally, each mandible exhibits an asetose baso-medial ventral groove (vg), and a medio-lateral sensory groove (sg).

The occlusal area of the left mandible in dorsal aspect (Fig. 2A) exhibits: a dorsal supraterebral ridge (str): terebral ridge (tr), terminated in a blunt terebral tooth (tt) that is evident or not. Posterad the terebral tooth is the combined retinacular area (r-m). In most carabid groups, the retinaculum, with its posterior tooth, is distinct from the molar area. Ventrally, the occlusal

TABLE I. Diagnostic features of adult mandibles of New World species groups of *Coptodera* Dejean.

Species Group	TRL/OL[1]	BW/OL[2]	Terebral Strigils	Left Mandible				Right Mandible		
				Terebral Groove	Retinacular Groove	Ventral Groove	Molar Groove	Retinacular Surface	Post. Retin. Area	Terebral Groove
sallei	0.64	0.38	short, not ext. to str[3]	smooth	smooth	present	triang., base broad	smooth	narrow	smooth
aurata	0.64	0.43	short, not ext. to str	smooth	smooth	present	triang., base broad	smooth	narrow	smooth
elongata	0.66	0.39	short, not ext. to str	smooth	finely strigose	present	triang., base broad	smooth	narrow	smooth
depressa	0.64	0.47	short, not ext. to str, shallow	finely strigose	smooth	present	triang., base broad	smooth	narrow	smooth
transversa	0.70	0.40	short, ext. to str	strigose	strigose	present (very small)	linear, base narrow	strigose	widened slightly	strigose
festiva	0.63	0.46	short, not ext. to str	strigose	finely strigose	absent	linear, base narrow	smooth-strigose	widened slightly	strigose
aeneorufa	0.58	0.43	long, ext. to str	strigose	finely strigose	present	linear, base narrow	strigose	widened moderately	strigose
bifasciata	0.63	0.41	short, not ext. to str, shallow	strigose	strigose	present	linear, base narrow	smooth-strigose	widened slightly	strigose
emarginata	0.55-0.58	0.44-0.45	short-long, ext. to str	strigose	finely strigose	present	linear, base narrow	smooth	widened moderately	strigose
picea	0.55	0.52	long, ext. to str	strigose	strigose	present	linear, base narrow	deeply strigose	widened markedly	strigose
aerata	0.59-0.62	0.47-0.49	long, ext. to str	strigose	strigose	present	narrowly triang.	smooth	widened moderately	strigose

[1] TRL/OL: Length of terebral margin/overall length
0.55-0.58, terebra relatively short
0.59-0.62, terebra moderately long
0.63-0.66, terebra elongate

[2] BW/OL: Width at base/overall length
0.38-0.42, molar area relatively narrow
0.43-0.47, molar area relatively intermediate
0.48-0.52, molar area relatively broad

[3] str: Supraterebral ridge

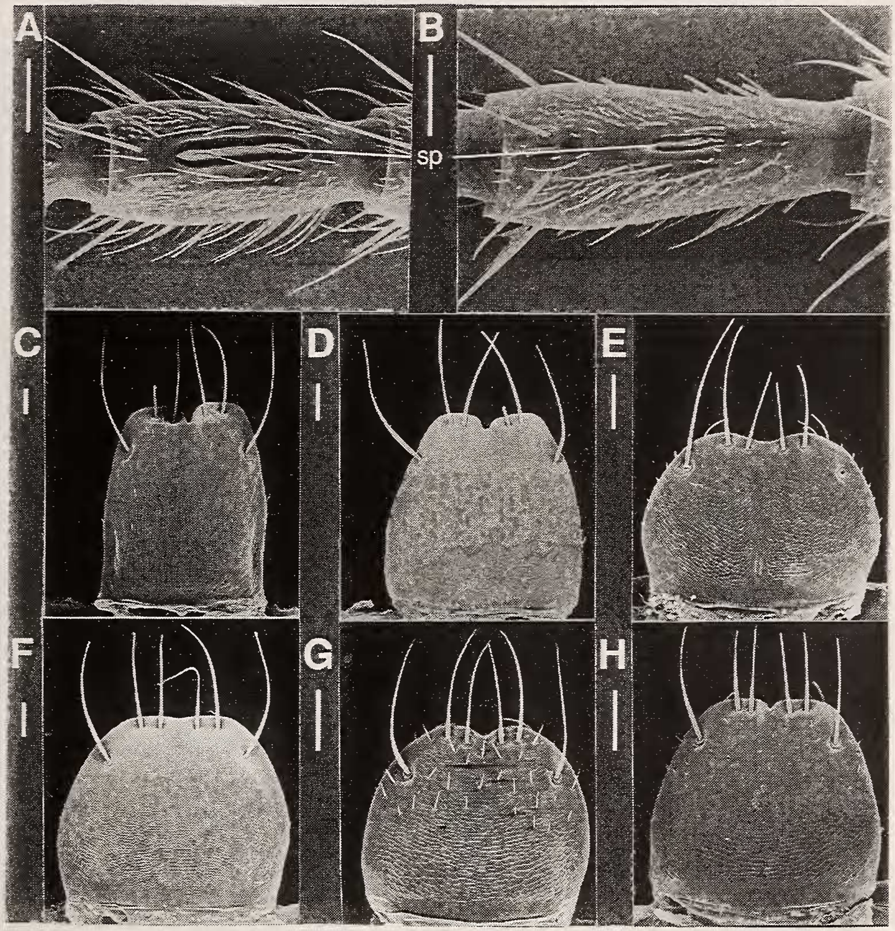


FIGURE 1. SEM photographs of structures of *Coptodera*. Figs. A-B, antennomere 8, ventral aspect. Fig. A: *C. nitidula* (Buquet). Fig. B: *C. brunnea*, new species. Figs. C-H, labrum, dorsal aspect. Fig. C: *C. championi* Bates. Fig. D: *C. xanthopleura* Bates. Fig. E: *C. festiva* Dejean. Fig. F: *C. acutipennis* (Buquet). Fig. G: *C. nitidula* (Buquet). Fig. H: *C. aerata* Dejean. Scale bars: Figs. A-B = 50 μm; Figs. C-H = 100 μm. Legend: sp, sensory pit.

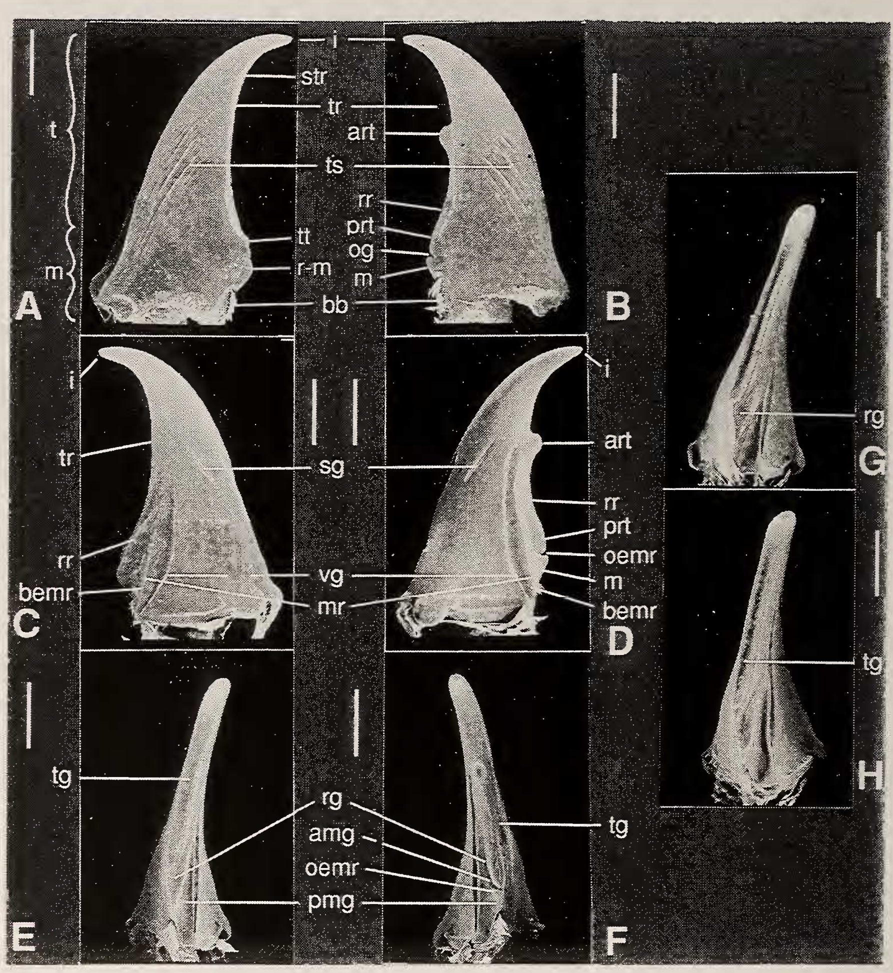


FIGURE 2. SEM photographs of mandibles of *Coptodera* species. Figs. A & C left, dorsal and ventral aspects respectively. Figs. E, G & H left, occlusal aspects. Figs. B, D & F right, dorsal, ventral and occlusal aspects respectively. Figs. A-F: *C. sallei*, new name. Fig. G: *C. championi* Bates. Fig. H: *C. versicolor* Bates. Scale bars = 200 μm. Legend: amg, anterior molar groove; art, anterior retinacular tooth; bb, basal brush; bemr, basal extension of the molar ridge; i, incisor; m, molar area; mr, molar ridge; oemr, occlusal extension of the molar ridge; og, occlusal groove; pmg, posterior molar groove; prt, posterior retinacular tooth; rg, retinacular groove; r-m, retinacular area; rr, retinacular ridge; sg, sensory groove; str, supraterebral ridge; t, terebra; tg, terebral groove; tr, terebral ridge; ts, terebral strigils; tt, terebral tooth; vg, ventral groove.

area includes a retinacular ridge (rr), the sole identifiable remnant of the retinaculum, and a molar ridge (mr), with basal extension (bemr) (In most carabids, an occlusal extension intersects the occlusal margin, marking the separation between molar area and retinaculum).

The occlusal margin of the right mandible exhibits in dorsal aspect (Fig. 2B) a terebral ridge without clear indication posteriorly of a terebral tooth. Ventrad the terebral ridge is the retinaculum, comprising an anterior tooth (art), a ridge (rr), and a posterior portion that is expanded or not (prt). Posteriorly, the molar area (m) is separated from the retinaculum by a shallow groove (og), and an occlusal extension of the molar ridge (oemr). Ventrally, the molar ridge exhibits also a basal extension (bemr).

In occlusal aspect on the left mandible (Fig. 2E), a terebral groove (tg) between supraterebral and terebral ridges extends the length of the terebra. Posterad the terebral groove is a short triangular depression, the retinacular groove (rg), which, because of the absence of the occlusal extension of the molar ridge, is co-extensive with an anterior molar groove (amg). Posterad the retinacular groove is a posterior molar groove (pmg).

In the occlusal aspect of the right mandible (Fig. 2F) the same grooves as on the left mandible are indicated, but the anterior molar groove and retinacular groove are separated from one another.

Labium.-- The word "*ligula*" is used for glossae + paraglossae. In turn, the fused, sclerotized glossae, characteristic of carabids, are termed collectively the "*glossal sclerite*" (Ball and Shpeley 1983: 746).

Elytra.-- Longitudinal grooves on the dorsal surface (striae of most authors) are designated as "*interneurs*" (Erwin 1974: 3-5), Cooper's (1990) arguments to the contrary notwithstanding.

Male genitalia.-- Median lobes were classified as: anopic (ostium dorsad); catopic (ostium ventrad); pleuropic (ostium lateral and internal sac directed lateral in everted position), left or right. Extent of membranous portion was expressed as length of membranous portion/length of median lobe. Values obtained were classified as follows: short, 0.19-0.28; medium-short, 0.29-0.37; medium, 0.38-0.46; medium-long, 0.47-0.55; and long, 0.56-0.63. Similarly, the apical portion of the median lobe was classified as: very short, 0.02-0.06; short, 0.07-0.10; medium-short, 0.11-0.14; medium, 0.15-0.21; medium-long, 0.22-0.25; and long, 0.26-0.29. These terms were used in the descriptions rather than the actual measurements.

Ovipositor.-- Ball and Shpeley (1983: 746) explain terms used for sclerites and setae, and orientation, of this structure. Note that for the stylomeres, the surfaces that are ventral in the infolded position are lateral when the ovipositor is extended; thus such surfaces are designated as lateral, and the other surfaces are designated accordingly.

Geographical terms

An important landmark that extends north-south in South America is the Andean mountain system. Areas to the west of the Andes are designated *trans*-Andean; those to the east, as *cis*-Andean. The term *Middle America* is used to refer to México + the republics of Central America, collectively. To facilitate zoogeographic discussion, the following terms are used: *Nuclear Middle America*, which includes northern Nicaragua, the Central American republics north thereof and México; *Lower Central America*, which includes the southern part of Nicaragua, Costa Rica and Panamá, a region which, until the Pliocene epoch, consisted of a series of isolated volcanic islands; and *Nuclear Central America*, which includes northern Nicaragua, Honduras, El Salvador and Guatemala, and México south of the Isthmus of Tehuantepec. For South America, two general areas are distinguished: Northern South America, to the north of the Tropic of Capricorn; and Southern South America, to the south of that parallel of latitude. See also Table XV and Map 21 for delimitation of reference areas in South America.

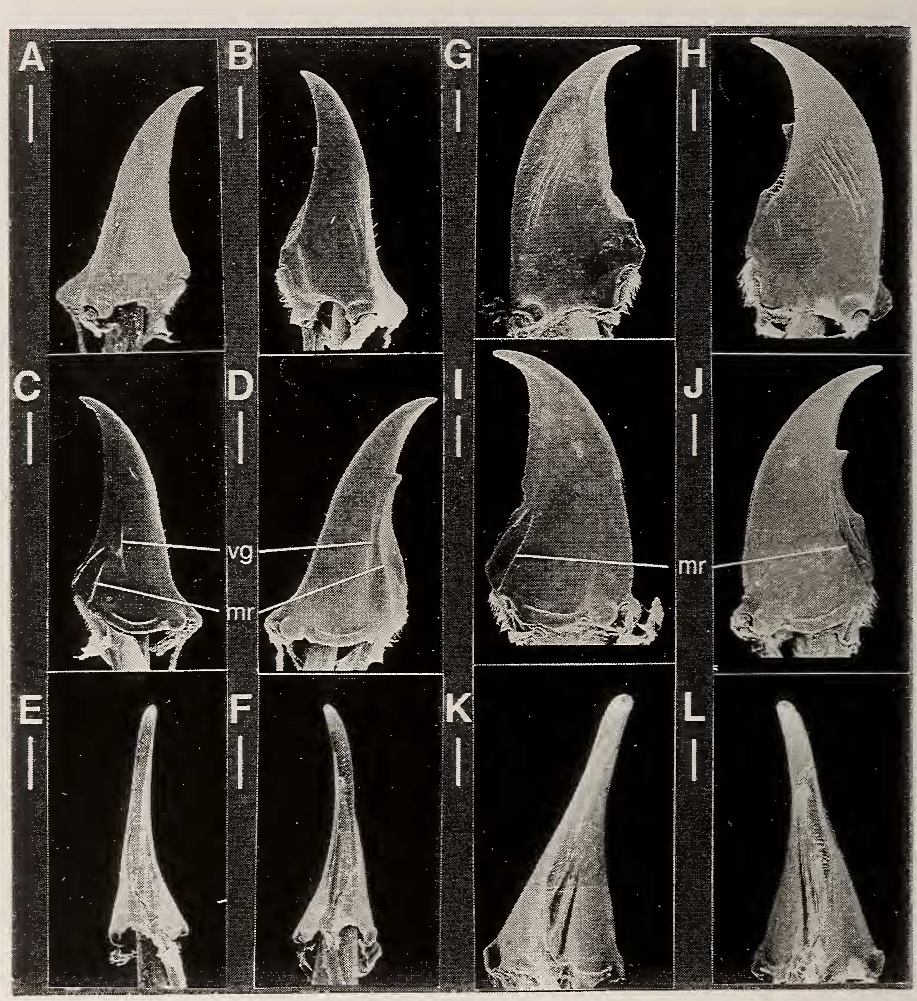


FIGURE 3. SEM photographs of mandibles of *Coptodera* species. Figs. A & G, C & I and E & K left, dorsal, ventral and occlusal aspects respectively. Figs. B & H, D & J and F & L right, dorsal, ventral and occlusal aspects respectively. Figs. A-F: *C. transversa* (Reiche). Figs. G-L: *C. festiva* Dejean. Scales bars = 100 μm. Legend: mr, molar ridge; vg, ventral groove.

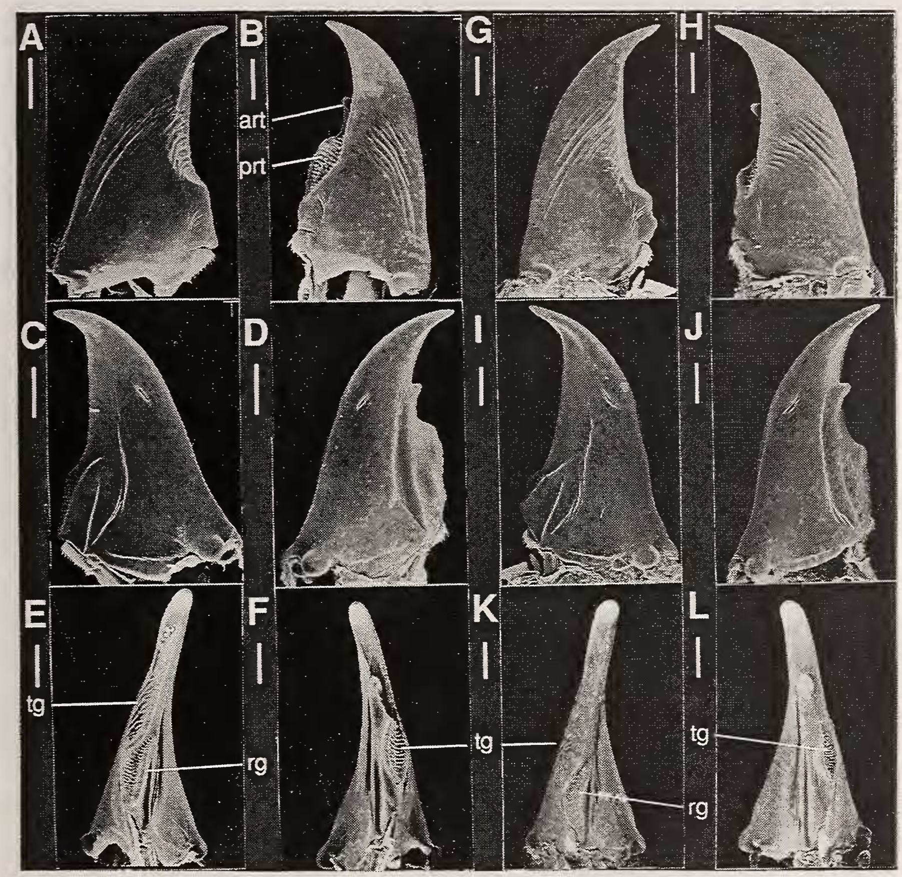


FIGURE 4. SEM photographs of mandibles of *Coptodera* species. Figs. A & G, C & I and E & K left, dorsal, ventral and occlusal aspects respectively. Figs. B & H, D & J and F & L right, dorsal, ventral and occlusal aspects respectively. Figs. A-F: *C. picea* Dejean. Figs. G-L: *C. nitidula* (Buquet). Scales bars = 100 μm. Legend: art, anterior retinacular tooth; prt, posterior retinacular tooth; rg, retinacular groove; tg, terebral groove.

Biogeographical terms

Frank and McCoy (1990) argue that the term "endemic" is restricted most appropriately to its original meaning as a descriptor of populations, the antonym of "epidemic", and implying nothing about native origin. To refer to taxa, they recommend the use of "indigenous" (synonyms: autochthonous, native) for a taxon that achieved its current taxonomic status in the area where it is living. If an indigenous taxon occurs nowhere else, it is referred to as "precinctive" (from Latin, *precinctus*, present participle of *praecingere*, to gird, or encircle).

A taxon that achieved its taxonomic status elsewhere than in a given area where it occurs now, is "adventive" in that area. An adventive taxon is either "introduced" if moved to a given area by man; or it is "immigrant" if it was not introduced.

We find the arguments presented by Frank and McCoy to be cogent and compelling, and adopt here their recommendations.

Phylogenetic terms

Those used are standard, except for "*adelphotaxon*". This word was introduced by Ax (1987: 36) as a substitute for "sister taxon", "sister group". The advantage of using adelphotaxon is that, being of classical origin, it will be the same in all European languages.

Classification

The *Pericalus* Genus-Group

This grouping is equivalent to the Coptoderinae of Jeannel (1949) and Hansen (1968), the "pericaloid assemblage" of Ball and Shpeley (1983: 751), and the tribe Pericalini (Basilewsky 1984: 542).

Recognition.-- This group is characterized by the following features of adults: palpigers setigerous (Fig. 5, each palpiger with one long seta inserted ventrally) and stylomere 2 of the ovipositor (Fig. 12) with very short nematiform setae.

Two genera are included: *Coptodera* Dejean, and *Pericalus* Macleay. Of the two, only *Coptodera* inhabits the New World.

Coptodera Dejean

Coptodera Dejean 1825: 273. TYPE SPECIES: *Coptodera festiva* Dejean 1825: 274. (Subsequent designation, Hope 1838: 85).-- Blanchard 1842: 118, plate 20.-- Duponchel 1844: 202.-- Lacordaire 1854: 140.-- Bates 1869: 71.-- Chaudoir 1869: 163.-- Horn 1881: 156.-- Bates 1883: 180-183.-- Leng 1920: 66.-- Csiki 1932: 1370.-- Darlington 1934: 116.-- Blackwelder 1944: 57.-- Jeannel 1949: 924, 926.-- Ball 1960: 158.-- Habu 1967: 81.-- Darlington 1968: 110.-- Darlington 1971: 194.-- Reichardt 1972: 238.-- Ball 1975: 176.-- Reichardt 1977: 446.-- Erwin & Sims 1984: 398.-- Basilewsky 1984: 542.

Stenoglossa Chaudoir 1848: 116. NEW SYNONOMY. TYPE SPECIES (by monotypy): *Stenoglossa variegata* Chaudoir 1848: 117.-- Lacordaire 1854: 141.-- Bates 1869: 71, 77.-- Chaudoir 1869: 201.-- Bates 1883: 184.-- Csiki 1932: 1375.-- Blackwelder 1944: 58.-- Ball 1975: 172.-- Reichardt 1977: 446.

Haplocrepis Jeannel 1949: 926. NEW SYNONYMY. TYPE SPECIES (original designation): *Coptodera hova* Alluaud 1936: 9.-- Hansen 1968: 346.-- Reichardt 1977: 446.-- Basilewsky 1984: 542.

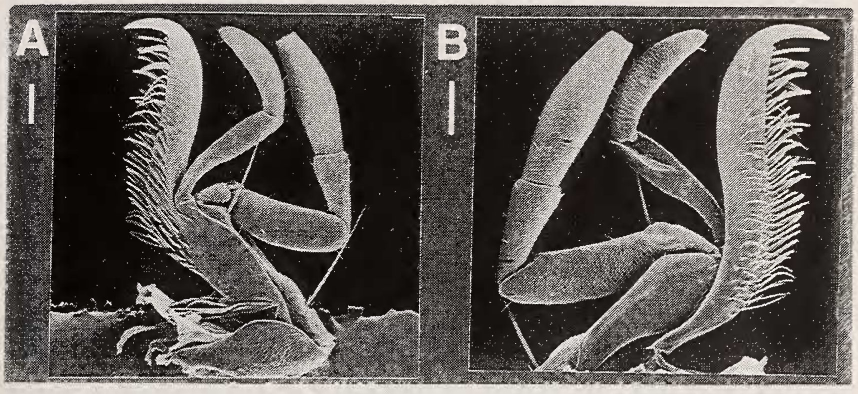


FIGURE 5. SEM photographs of maxilla of *C. sallei*, new name. Figs. A & B dorsal and ventral aspects respectively. Scale bar = 100 μm.

Derivation of generic name.-- From two Greek words: *copto*, cut; and *dere*, neck; in allusion to the straight posterior margin of the pronotum, which seems to have been cut abruptly (Dejean 1825: 273). This is in contrast to the lobed base of the pronotum that is characteristic of *Lebia* adults. Dejean, in proposing *Coptodera*, removed from *Lebia* those species with straight posterior pronotal margins.

Note about type designation.-- Most researchers have listed *Coptodera festiva* Dejean as the type species of *Coptodera* Dejean, a selection made by Hope (1838) and by Duponchel (1844). Blanchard (1842) designated *Coptodera emarginata* Dejean as the type species of *Coptodera* in Plate 20. This designation is invalid by virtue of the principle of priority.

Notes about synonymy.-- Bates (1869: 77-78) noted that specimens of *Stenoglossa* hardly differed from those of *Coptodera* in mouthparts (the basis used by Chaudoir for proposing the former genus), though the lobed base of the pronotum was distinctive. Nonetheless, he wrote that: "Several *Coptoderae* show a trace of the basal lobe, and it is doubtful that the present genus (*i.e. Stenoglossa*) can be maintained. The species have precisely the same habits as the *Coptoderae*." Ball (1975: 172) excluded *Stenoglossa* from the pericaloid assemblage and placed it with the eurycoleoids, though he wrote that: "It is not certain that *Stenoglossa* belongs here..." Although Ball noted the similarity between stylomere 2 exhibited by *Stenoglossa* and *Coptodera* females, he believed the palpigers of the former to be asetose, and so excluded it from the pericaloid assemblage. Basilewsky (1984: 542) suggested that *Stenoglossa* was a pericaloid, even though its palpigers were asetose.

Careful examination showed, in fact, that the palpigers of *Stenoglossa* adults were setigerous. In view of Bates' remarks and our own studies, we are satisfied that *Stenoglossa* and *Coptodera* (*sensu latissimi*) are indeed congeneric.

Jeannel (1949: 926) proposed the genus *Haplocrepis* to accommodate the Madagascan *Coptodera hova* Alluaud, several other Madagascan species, and the Neotropical species *C.*

nubiculosa Chaudoir. The principal character states distinguishing *Haplocrepis* from *Coptodera* were: structure of the median lobe (anopic in *Haplocrepis*), and adult body size (small in *Haplocrepis*). The anopic condition of the male genitalia is likely to be plesiotypic, and thus would not provide good evidence about relationships. Small size is not very convincing, either. Furthermore, *C. nubiculosa* (= *C. nitidula* Buquet) differs from the Madagascan males of *Haplocrepis* by having spines on the internal sac, and by having a much larger apical orifice. It seems doubtful, therefore, that *C. nubiculosa* and *C. hova* belong to the same species group.

More generally, the condition of the median lobe (anopic, pleuropic, catopic) is varied sufficiently among the taxa of the *Pericalus* genus group that such a feature is not a good one to use for making distinctions at the genus level. Concerning *C. nubiculosa*, it belongs to a phylogenetically derived species group of *Coptodera*. For these reasons, the species assigned to *Haplocrepis* by Jeannel and Hansen are regarded as congeneric with those of *Coptodera*.

Diagnosis.-- New World adult *Coptodera* are readily separated from other genera in the subtribe Pericalina by a combination of three character states: mentum without a medial tooth; mandibles not explanate along ventral-lateral margin basally; and labial palpiger setose (Figs. 6A-D).

Limits of the genus.-- We include in *Coptodera* all pericaline taxa with adults characterized by setigerous labial palpigers, and pectinate tarsal claws, *i.e.*, the Coptoderinae of Jeannel (1949) and Hansen (1968), plus various Oriental elements, such as *Lioptera* Chaudoir and *Brachytis* Chaudoir. Because these coptoderine genera are in the Old World, and because the present treatment concerns the New World species only, we have not provided a complete generic synonomy. At some future date, we expect to offer a detailed treatment of the Old World taxa.

Description.-- Form narrow, elongate to moderately wide in relation to length; somewhat flattened to slightly robust. Size various, from small to moderate (SBL 3.80-11.08 mm; Table II).

Color. Dorsal surface dark testaceous to piceous, metallic or not; elytra concolorous, or bicolored, most specimens with pale markings on dark background. Ventral surface, antennae and mouthparts testaceous to rufo-piceous; appendages testaceous to piceous, concolorous or bicolored.

Microsculpture. Microlines of various depth; sculpticells moderately convex to flat. Meshes of labrum, clypeus and head isodiametric; meshes of pronotum isodiametric to moderately transverse, microlines effaced on the disc of some species; meshes of elytra isodiametric to markedly transverse (not iridescent), microlines nearly effaced in some species; meshes of ventral surface isodiametric to markedly transverse (not iridescent), microlines nearly effaced in some species.

Luster. Moderately shining to brilliant, not iridescent.

Fixed setae. As in Lebiini and head with one pair of suborbital setae. Glossal sclerite with two long setae apically. Penultimate labial palpomere bisetose on inner margin near apex; palpiger with a single seta. Disc of elytron with three to four setigerous punctures in third interval. Umbilical series with 14 or more setigerous punctures, setae of different lengths.

Head. Eyes large, subgena markedly reduced. Frons varied, from smooth to markedly wrinkled with longitudinal carinae. Antennomeres 5-11 each with (Figs. 1A-1B) or without sensory pit on ventral surface.

Mouthparts. Labrum (Figs. 1C-1H) elongate to transverse; anterior margin notched medially, or shallowly to deeply emarginate medially. Mandibles (Figs. 2-4) are discussed in detail in the section "Terms for structural features". Maxilla (Fig. 5) average for Lebiini. Labium (Fig. 6) with paraglossae markedly developed; dorsal surface of paraglossae with or without spines.

Prothorax. Pronotum moderately broad (Hw/Pw 0.71-1.21); width greater than length (Pw/Pl 1.38-1.94), widest in anterior half; anterior margin straight to moderately emarginate; lateral

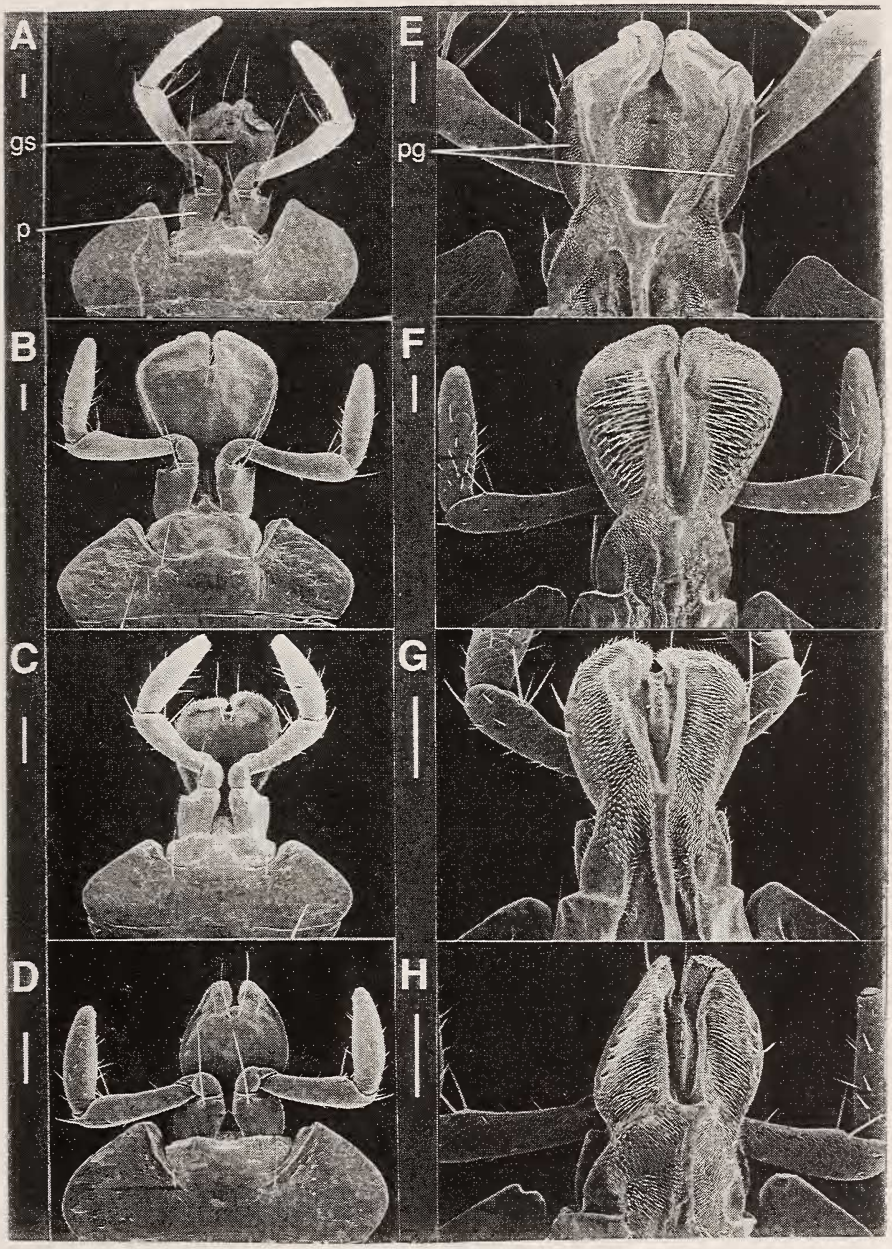


FIGURE 6. SEM photographs of labium of *Coptodera* species. Figs. A-D ventral aspect. Figs. E-H dorsal aspect. Figs. A & E: *C. championi* Bates. Figs. B & F: *C. acutipennis* (Buquet). Figs. C & G: *C. picea* Dejean. Figs. D & H: *C. aerata* Dejean. Scale bars = 100 μm. Legend: gs, glossal sclerite; p, palpiger; pg, paraglossae.

margin slightly rounded, straight or sinuate posteriorly; posterior margin straight (Fig. 7A), slightly convex (Fig. 7C-7D), or lobed (Fig. 7B); hind angles acute to obtuse; disc moderately convex to nearly flat; median longitudinal depression linear, faintly to moderately impressed; lateral grooves narrow to moderately wide; posterior margin beaded. Propleura and prosternum average for Lebiini.

Pterothorax. Average for Lebiini; metepisternum elongate, with lateral margin much longer than width at anterior margin; metepimeron with posterior margin obliquely truncate.

Elytra. Humerus rounded; sides nearly parallel to widened apically; apical margin subtruncate. Apex with lateral and sutural angles spinose or not. Basal ridge complete; lateral margins moderately explanate. Interneurs shallow, punctate to impunctate. Intervals flat to convex.

Hind wings. Fully developed, with large oblongum cell and wedge cell.

Legs. Fore-tibia with markedly reduced to markedly developed upper spur on inner surface. Males with ventral surface of mid-tibia with blunt denticles or notched near apex. Tarsomeres with dorsal surfaces setose. Males with tarsomeres 1-3 of fore-leg with adhesive vestiture, and tarsomeres 2-3 of mid-leg with or without adhesive vestiture. Tarsal claws pectinate, pectens large (Fig. 9H) to small (Fig. 9B).

Habitat range.-- *Coptodera* species were collected at 30 to 2300 m altitude, in most forest types, that range from dry thorn forest to wet cloud forest. Most specimens were taken on standing or fallen tree trunks, living vegetation and also on the ground at fruitfalls.

Relationships.-- *Coptodera* is postulated here to be the adelphotaxon of *Pericalus*.

Classification of the New World species.-- The 43 New World species of *Coptodera* are arranged in 11 species groups (Table I), each postulated to be monophyletic.

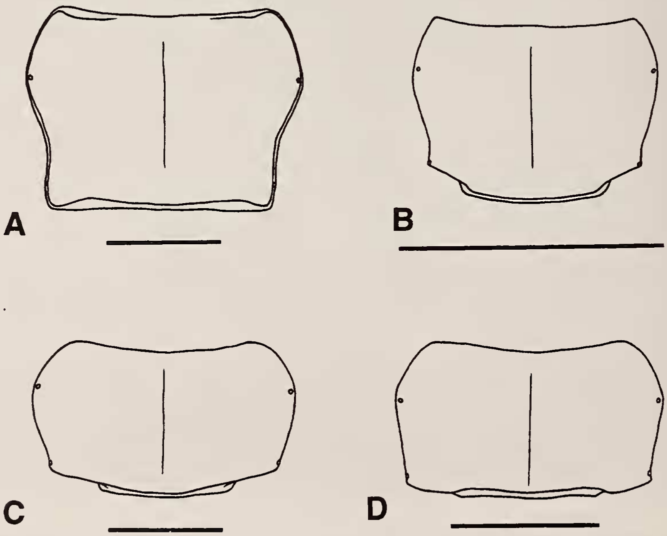


FIGURE 7. Line drawings of pronota of *Coptodera* species, dorsal aspect, lateral setae omitted. Fig. A: *C. apicalis*, new species. Fig. B: *C. stockwelli*, new species. Fig. C: *C. sahlbergi* Chaudoir. Fig. D: *C. teutonica*, new species. Scale bars = 1 mm.

TABLE II. Variation in SBL among males of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	6.33-7.25	6.82
C. elongata Putzeys	México	10	9.42-11.00	9.98
C. schaumi Chaudoir	Costa Rica	4	8.25-9.00	8.79
C. megalops Bates	Bolivia	10	6.58-9.25	8.22
C. championi Bates	Panamá	10	7.25-8.92	8.17
C. apicalis, new species	Colombia	4	6.83-9.00	7.58
	Ecuador	10	7.50-9.75	8.64
C. xanthopleura Bates	México	10	5.68-7.40	6.28
C. aurata Chevrolat	México	9	6.28-7.52	7.03
C. viridis, new species	Panamá	7	6.08-7.42	6.57
C. depressa Dejean	Brazil	10	6.83-8.33	7.87
C. versicolor Bates	Brazil	3	6.25-7.75	7.19
	Peru	3	7.67-7.92	7.81
C. dromioides Bates	Brazil	6	3.50-3.94	3.75
C. nigrosignata Chaudoir	Brazil	4	2.66-3.22	2.99
C. fulminans Bates	Brazil	2	3.14-3.36	3.25
C. nigrostriata Reiche	Bolivia	2	3.46-3.66	3.56
	Brazil	4	3.30-3.92	3.63
C. lineata Bates	México	10	2.76-3.04	2.92
C. stockwelli, new species	Panamá	10	3.08-3.42	3.20
C. transversa Reiche	México	10	2.76-3.02	2.93
C. sigillata, new species	Brazil	1	3.80	3.80
C. sahlbergi Chaudoir	Brazil	4	5.32-6.20	5.81
C. relucens Bates	Brazil	2	5.72-5.84	5.78
C. poecila Bates	Panamá	1	4.64	4.64
C. festiva Dejean	México	10	4.80-5.96	5.13
C. foveolata, new species	México	2	4.84-5.72	5.28
C. nigroviridis, new species	México	1	6.88	6.88
C. rufescens Buquet	Brazil	1	9.33	9.33
C. teutonica, new species	Brazil	1	5.44	5.44
C. aeneorufa Bates	Brazil	6	5.33-6.50	6.04
C. bifasciata Putzeys	Brazil	2	5.88-5.92	5.90
C. tripartita Chaudoir	Brazil	5	5.28-5.88	5.64
C. cupreotincta Bates	Panamá	10	5.83-7.08	6.68
C. braziliensis, new species	Brazil	4	6.42-7.00	6.71
C. chalcites Bates	Brazil	6	6.58-8.83	7.82
	Peru	8	6.92-8.42	7.56
C. emarginata Dejean	Brazil	5	8.75-9.67	9.15
C. acutipennis Buquet (see Table VIII)				
C. picea Dejean	México	10	4.60-5.20	4.91
C. nitidula Buquet	Ecuador	10	4.16-5.40	4.61
C. brunnea, new species	U.S.A.	10	5.36-6.28	5.85
C. aerata Dejean	U.S.A.	10	4.96-5.68	5.35
C. waytkowskii Liebke	Brazil	3	5.32-5.76	5.48

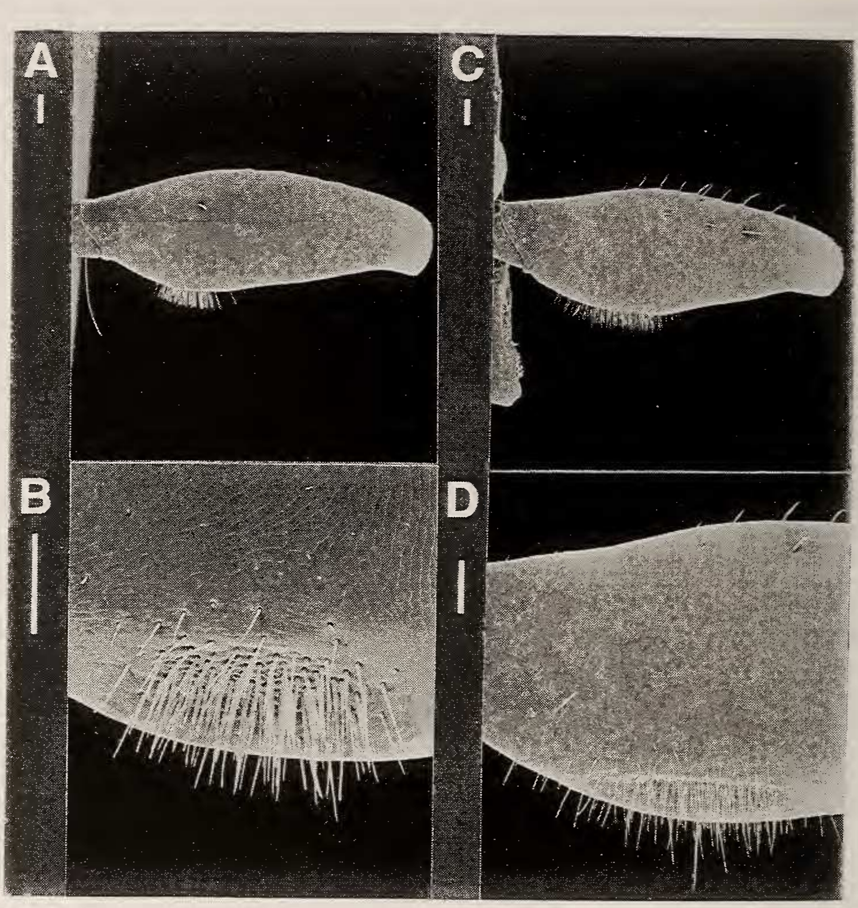


FIGURE 8. SEM photographs of fore-femur of *Coptodera* species, posterior aspect. Figs. A-B: *C. sallei*, new name. Figs. C-D: *C. versicolor* Bates. Scale bars = 100 µm.

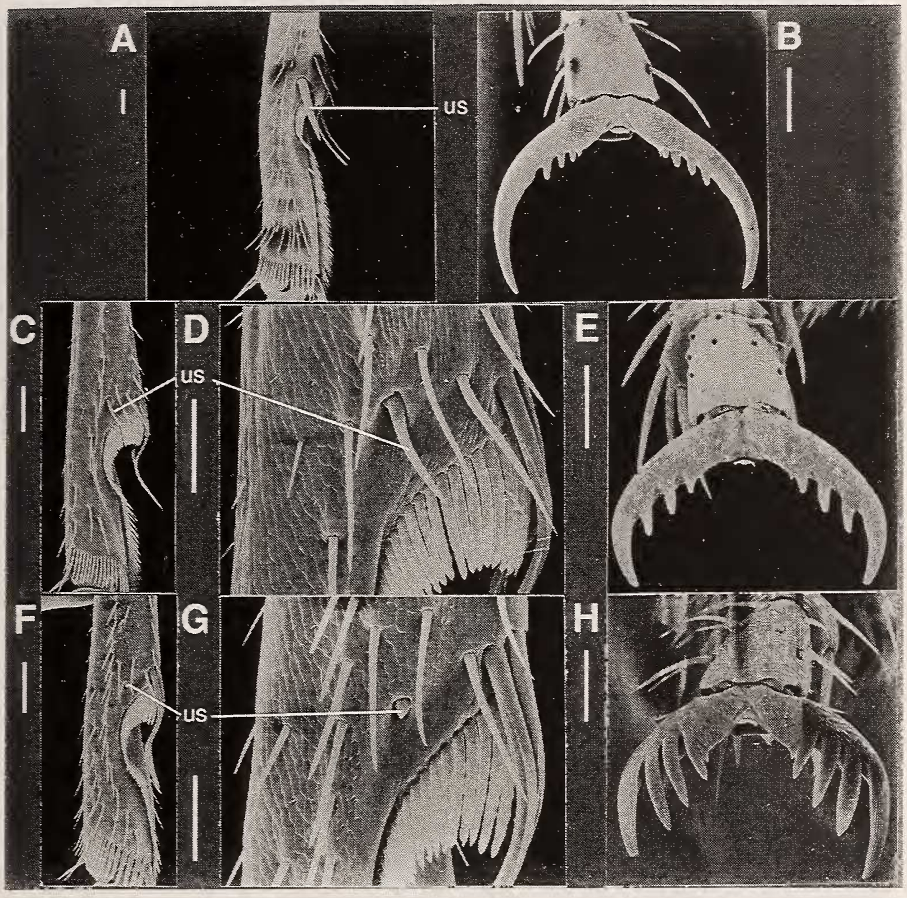


FIGURE 9. SEM photographs of structures of *Coptodera* species. Figs. A, C, D, F & G foretibia, posterior aspect. Figs. A: *C. championi* Bates. Figs. C-D: *C. picea* Dejean. Figs. F-G: *C. nitidula* (Buquet). Figs. B, E & H tarsal claws, terminal aspect. Fig. B: *C. championi* Bates. Fig. E: *C. picea* Dejean. Fig. H: *C. nitidula* (Buquet). Scale bars: Figs. A-C & F = 100 μm; Figs. D, E, G & H = 50 μm. Legend: us, upper spur.

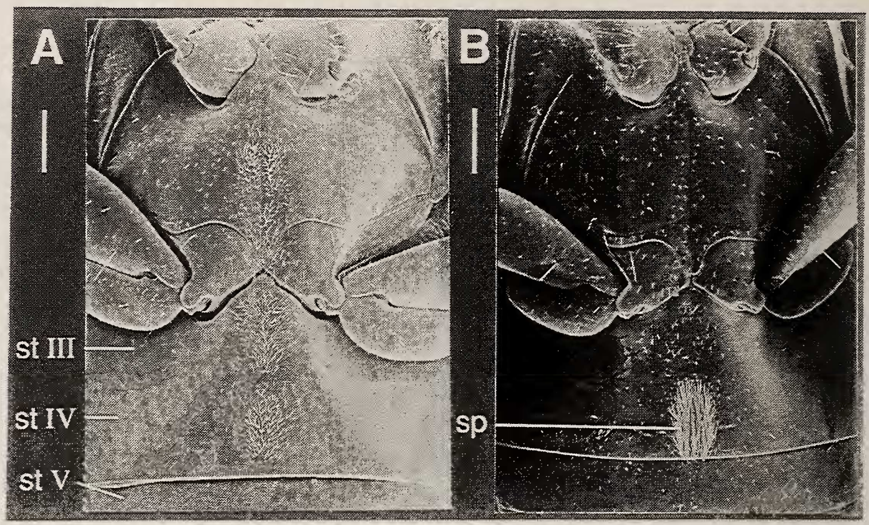


FIGURE 10. SEM photographs of abdominal sterna of *Coptodera* species, ventral aspect. Fig. A: *C. nigrostriata* (Reiche). Fig. B: *C. transversa* (Reiche). Scale bars = 200 μm. Legend: sp, setal patch; st, sternum.

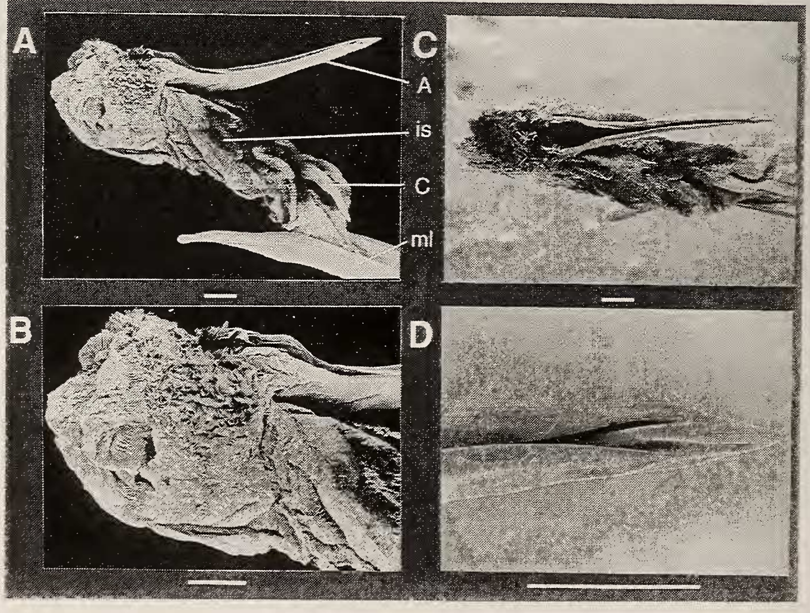


FIGURE 11. SEM photographs of male genitalia of *C. acutipennis* (Buquet), morph J. Fig. A & C and B internal sac, right lateral and dorsal aspects respectively. Fig. D apex of spine A, dorsal aspect. Scale bars = 100 μm. Legend: A, spine A; C, spine C; is, internal sac; ml, median lobe; sp, spine.

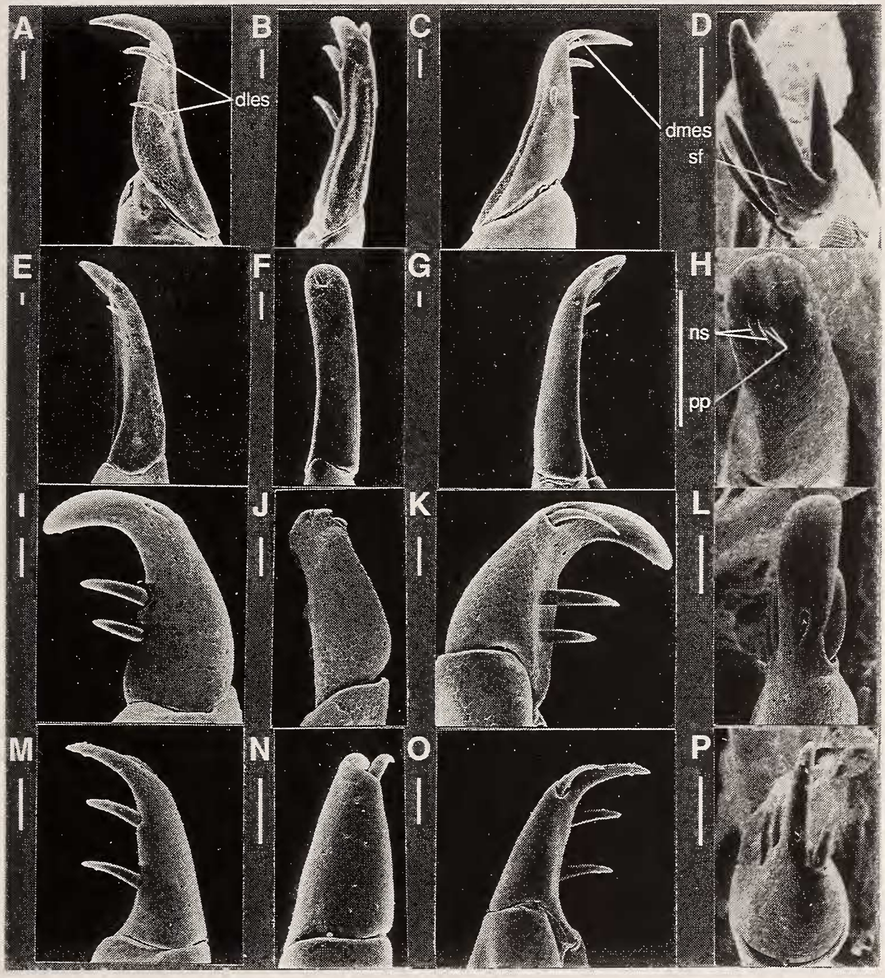


FIGURE 12. SEM photographs of stylomere 2 of ovipositor of *Coptodera* species. Figs. A, E, I & M lateral aspects. Figs. B, F, J & N ventral aspect. Figs. C, G, K & O medial aspect. Figs. D, H, L & P apical aspect. Figs. A-D: *C. championi* Bates. Figs. E-H: *C. transversa* (Reiche). Figs. I-L: *C. rufescens* Buquet. Figs. M-P: *C. aerata* Dejean. Scale bars = 50 μm. Legend: dles, dorsolateral ensiform setae; dmes, dorsomedial ensiform setae; ns, nematiform setae; pp, pit pegs; sf, sensory furrow.

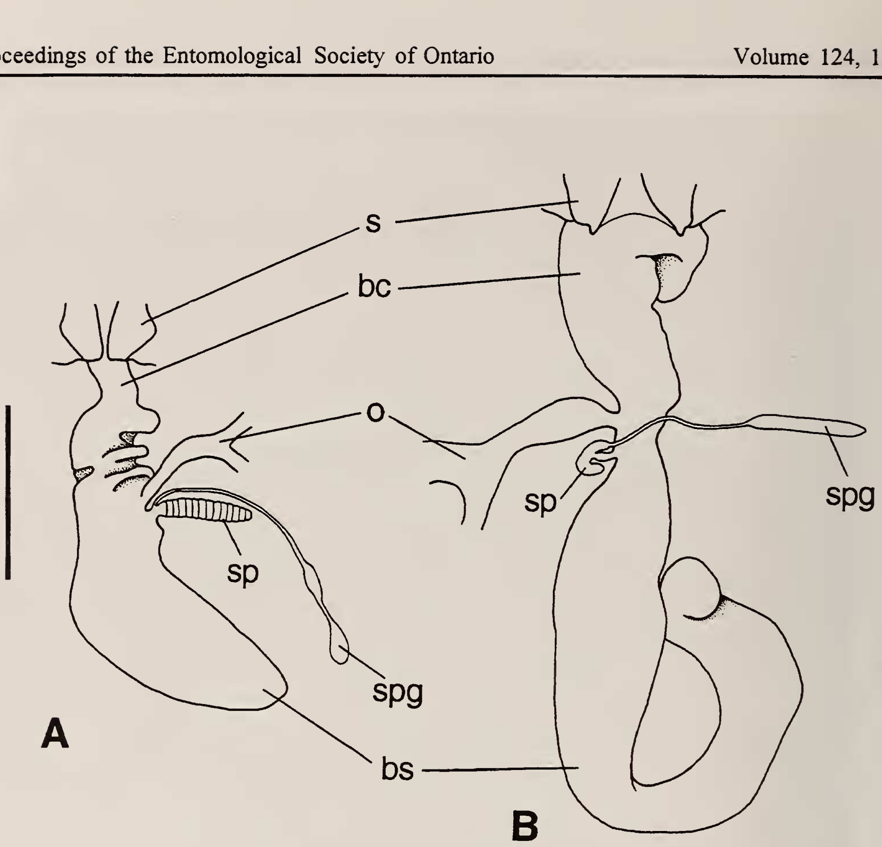


FIGURE 13. Line drawings of female reproductive tract, ventral aspect. Fig. A: *C. elongata* Putzeys. Fig. B: *C. acutipennis* (Buquet). Scale bars = 1 mm. Legend: bc, bursa copulatrix; bs, blind sac; o, oviduct; s, base of stylomere 1; sp, spermatheca; spg, spermathecal gland.

Abdominal sterna. Average for Lebiini. Sternum III and IV with or without scattered or dense setal patches. Sternum VII of males and females with 2 pair of apical setae; apical margin broadly rounded, shallowly notched, or deeply notched.

Male genitalia. Median lobe catopic, pleuropic (hemiopic left or right), or anopic. Internal sac with or without macro spines. "Sperm pump" sclerite associated with the ejaculatory duct.

Ovipositor (Fig. 12). Stylomere 2 about subfalcate, base not lobed; apex of S2 broadly rounded or narrowed. Ensiform setae moderately long, one dorsomedial and two or three dorsolateral; nematiform setae short or absent.

Female genitalia (Fig. 13). Spermatheca very short to longer. "Blind sac" present as small bulge to elongate or bulbous, or not present. [Liebherr (1986: 7) assumes this asymmetric lobe of the bursa copulatrix to be an egg holder in *Agonum* Bonelli].

Geographical distribution.-- The range of *Coptodera* extends throughout the tropics of the world, and warm temperate areas of the New World, and of Eastern Asia. In the New World, *Coptodera* ranges from northern Argentina in cis-Andean South America to southern Michigan and Delaware, in eastern United States (Maps 1-20).

Key to Adults of Species of *Coptodera*

1		Elytron with 3 discal setigerous punctures in interval 3	2
1'		Elytron with 4 discal setigerous punctures in interval 3	15
2	(1)	Elytron with apico-sutural angle spinose	3
2'		Elytron with apico-sutural angle rounded or acute, but not spinose	6
3	(2')	Apical pale markings of elytron longer than basal pale markings (Fig. 15E)	*C. apicalis*, new species, p. 45
3'		Apical pale markings of elytron similar or shorter than basal pale markings	4
4	(3')	Elytron with basal pale marking of interval 4 as two distinct pale spots (Fig. 15D)	*C. championi* Bates, p. 45
4'		Elytron with basal pale marking of interval 4 as one long pale spot	5
5	(4')	Elytron with basal pale marking of interval 5 as two distinct pale spots (Fig. 15B)	*C. schaumi* Chaudoir, p. 38
5'		Elytron with basal pale marking of interval 5 as one short pale spot (Fig. 15C)	*C. megalops* Bates, p. 40
6	(2')	Apico-lateral angle of elytron sharply obtuse (Fig. 15A)	*C. elongata* Putzeys, p. 36
6'		Apico-lateral angle of elytron rounded	7
7	(6')	Antennomeres 5-11 each with ventral sensory pit (as in Fig. 1B)	8
7'		Antennomeres 5-11 without ventral sensory pits	9
8	(7)	Head and pronotum colored the same as elytra; specimen from United States	*C. aerata* Dejean, p. 118
8'		Head and pronotum rufo-testaceous, elytra piceous; specimen from Peru	*C. tripunctata*, new species, p. 179
9	(8')	Elytra unicolorous	10
9'		Elytra with variegated color pattern	12
10	(9)	Elytral microsculpture coarser, clearly transverse (sculpticells about 3-4 times as wide as long)	*C. xanthopleura* Bates, p. 49
10'		Elytral microsculpture fainter, isodiametric to slightly transverse, or nearly effaced, sculpticells not distinguishable	11
11	(10')	Elytral intervals flat; elytral microsculpture nearly effaced, without clear formation of sculpticells	*C. aurata* Chevrolat, p. 50
11'		Elytral intervals convex; elytral microsculpture isodiametric to slightly transverse	*C. viridis*, new species, p. 51
12	(8')	Elytron with sutural angle acute	*C. squiresi* (Chaudoir), p. 73
12'		Elytron with sutural angle rounded	12
13	(12')	Upper spur on inner surface of fore-tibia markedly reduced (as in Fig. 9G)	*C. transversa* (Reiche), p. 68
13'		Upper spur on inner surface of fore-tibia markedly developed	14
14	(13')	Larger in size (average SBL 6.54 mm); anterior margin of labrum notched medially	*C. sallei*, new name, p. 32
14'		Smaller in size (SBL 3.80mm); anterior margin of labrum shallowly emarginate medially	*C. sigillata*, new species, p. 70
15	(1')	Antennomeres 5-11 each with ventral sensory pit (Figs. 1A & 1B)	16
15'		Antennomeres 5-11 without ventral sensory pits	19

16 (14) Head with fine setae between posterior pair of supraorbital setae; elytron with apical pale markings only; tarsal claws each with two teeth . . . . *C. waytkowskii* Liebke, p. 122

16' Head without setae between posterior pair of supraorbital setae; elytron unicolorous to bicolored (without apical pale markings); tarsal claws each with three or four teeth 17

17 (16') Elytron with basal half pale, apical half piceous (Fig. 33E) . . . . *C. erwini*, new species, p. 122

17' Elytron unicolorous or with markings different than above 18

18 (17') Antennomeres 5-11 each with elongate ventral sensory pit (Fig. 1A); antennomeres unicolorous . . . . *C. nitidula* (Buquet), p. 112

18' Antennomeres 5-11 each with short ventral sensory pit (as in Fig. 1B); antennomeres 3 and 4 darker than adjacent antennomeres . . . . *C. brunnea*, new species, p. 116

19 (15') Apex of elytron with lateral angle sharply obtuse to spinose (Fig. 28B) 20

19' Apex of elytron with lateral angle rounded 21

20 (19) Intervals of elytron flattened; microsculpture of elytron nearly isodiametric; apex of elytron with short sinuation before spinose sutural angle (Fig. 28B) . . . . *C. emarginata* Dejean, p. 98

20' Intervals of elytron convex; microsculpture of elytron stretched to markedly transverse; apex of elytron at sutural angle not as above . . . . *C. acutipennis* (Buquet), p. 100

21 (19') Fore-tibia with markedly reduced upper spur on ventral surface . . . . *C. picea* Dejean, p. 108

21' Fore-tibia with moderately long upper spur on ventral surface 22

22 (21') Labrum deeply notched medially (as in Fig. 1C) 23

22' Labrum shallowly emarginate medially 24

23 (22) Elytral interneurs finely punctulate to impunctate . . *C. depressa* Dejean, p. 53

23' Elytral interneurs with rather large, easily seen punctures . . . . *C. versicolor* Bates, p. 55

24 (22') Elytra unicolorous 25

24' Elytra with variegated color pattern 26

25 (24) Elytral interneurs impunctate; elytron with apico-sutural angle narrowly rounded, nearly acute . . . . *C. aeneorufa* Bates, p. 87

25' Elytral interneurs distinctly punctate; elytron with apico-sutural angle broadly rounded (Fig. 28A) . . . . *C. chalcites* Bates, p. 97

26 (24') Interval 9 of elytron testaceous, with dark spots surrounding the medial umbilical setigerous punctures (Figs. 20D-20F) 27

26' Interval 9 of elytron testaceous or dark with only extreme lateral margin testaceous, without dark spots surrounding the medial umbilical setigerous punctures 29

27 (26) Elytral intervals 2 and 3 with dark transverse marking posteriad of discal seta #3 (Fig. 20E); upper spur on inner surface of fore-tibia markedly reduced . . . . *C. lineata* (Bates), p. 64

27' Elytral intervals 2 and 3 testaceous posteriad of discal seta #3 (Figs. 20D & 20F); upper spur on inner surface of fore-tibia markedly developed 28

28 (27') Specimen from Colombia or Brazil . . . . *C. nigrostriata* (Reiche), p. 62

28' Specimen from Panamá . . . . *C. stockwelli*, new species, p. 66

29 (26') Basal pale markings of elytron extensive, extended from suture to interval 8 (Figs. 20A-20C) 30

29' Basal pale markings of elytron present in interval 1 32

30 (29) Elytron with extensive dark markings (Fig. 20A) . *C. dromioides* (Bates), p. 59

30' Elytron with extensive pale markings (Figs. 20B & 20C) 31

31 (30') Apex of elytron nearly straight; dark markings of intervals 4 and 5 with posterior margins anteriad of discal seta #3 (Fig. 20B) . . . . *C. nigrosignata* Chaudoir, p. 61

31' Apex of elytron sinuate; dark markings of intervals 4 and 5 extended posteriad of discal seta #3 (Fig. 20C) . . . . *C. fulminans* (Bates), p. 61

32 (29') Basal pale markings in intervals 4 and 6 of elytron extended to apical pale markings in respective intervals (Fig. 23D) . . . . *C. poecila* Bates, p. 77

32' Basal and apical pale markings in intervals 4 and 6 of elytron separated by darker median transverse marking 33

33 (32') Tarsal claws long, with short denticulations in basal half only . . . . *C. rufescens* Buquet, p. 85

33' Tarsal claws shorter, with longer denticulations along length of claw 34

34 (33') Elytral interneurs punctate 35

34' Elytral interneurs impunctate 42

35 (34) Basal pale markings in intervals 6-8 of elytron divided into two, and extended to basal ridge (Fig. 23E) . . . . *C. pakitza*, new species, p. 78

35' Basal pale markings of elytron not extended to basal ridge 36

36 (35') Basal pale markings in intervals 6 and 7 of elytron elongate (Figs. 26C & 26D) 37

36' Basal pale markings in intervals 6 and 7 of elytron shorter in relative length 38

37 (36) Pronotum with broad testaceous lateral margins; apical pale markings of elytron in intervals 2-8 (Fig. 26C) . . . . *C. cupreotincta* Bates, p. 92

37' Pronotum unicolorous; apical pale markings of elytron in intervals 2-7 (Fig. 26D) . . . . *C. braziliensis*, new species, p. 94

38 (36') First basal pale marking in interval 3 or 4 of elytron (Figs. 23A, 23H & 23J) 39

38' First basal pale marking in interval 1 or 2 of elytron 41

39 (38) Specimen from México; pale markings of elytron reduced (Fig. 23H) . . . . *C. nigroviridis*, new species, p. 84

39' Specimen from South America; pale markings of elytron more extensive (Figs. 23A & 23J) 40

40 (39') Pronotum with base narrower at hind angles, and posterior margin distinctly convex (Fig. 7C) . . . . *C. sahlbergi* Chaudoir, p. 75

40' Pronotum with base wider at hind angles, and posterior margin nearly straight (Fig. 7D) . . . . *C. teutonica*, new species, p. 86

41 (37') Specimen from Brazil; disc of pronotum broadly pale medially; pale apical marking in interval 4 of elytron widely separated from basal pale marking in interval 5 (Figs. 23B & 23C) . . . . *C. relucens* Bates, p. 76

41’ Specimen from México; disc of pronotum dark; pale apical marking of elytron in interval 4 narrowly separated from basal pale marking of interval 5 (Fig. 23G) .... *C. foveolata*, new species, p. 83

42 (34’) Elytron with anterior margin of basal pale markings in intervals 4 and 6 extended equally, or that of interval 6 nearer basal ridge (Figs. 26A & 26B) 43

42’ Elytron with anterior margin of basal pale markings in intervals 4 and 6 unequal, that of interval 4 nearer basal ridge (Fig. 23F) .... *C. festiva* Dejean, p. 82

43 (42) Basal pale markings of elytron not extended laterally past interval 8 (Fig. 26A) .... *C. bifasciata* Putzeys, p. 90

43’ Basal pale markings of elytron extended to lateral margin (Fig. 26B) .... *C. tripartita* Chaudoir, p. 91

Coptodera sallei Group

This group has a single species, adults of which have notched anterior margin of labrum which is longer than wide, three discal setigerous punctures on each elytron, elytra with variegated pattern, elytral apices not spined, markedly developed upper spur on the inner surface of the fore-tibia, mid-tibia of male with blunt denticles on the ventral surface near the apex, and the fore-femur of males with a dense brush of setae on the ventral surface. See Table I for features of mandibles. Male genitalia median lobe left pleuropic-catopic, more pleuropic than catopic, membranous portion short; internal sac with row of macrotrichia (Figs. 14B-14C). Ovipositor with ensiform setae of stylomere 2 dorso-lateral (cf. Fig. 12A); nematiform setae present. The geographical range of this group is limited to México and Guatemala, in Middle America (Map 1).

Chorological affinities.-- The range of the *C. sallei* group is broadly overlapped in Nuclear Middle America by that of the *C. elongata* and *C. aurata* groups (Maps 1-5).

Phylogenetic relationships.-- This group is the adelphotaxon of the other groups of the 3-punctate lineage (lineage A, Fig. 35).

Coptodera sallei, new name

Figs. 2A-2F, 5, 8A, 8B, 14A-14C; Map 1

Coptodera variegata Chaudoir 1869: 168. Type material: LECTOTYPE (here selected) male, labelled: ♂; Ex Musaeo Chaudoir (red print); TYPE (red paper); LECTO- TYPE (disc with purple border); Coptodera variegata Chaud LECTOTYPE det. G.E. Ball ’72; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: México.

Coptodera sallei, NEW NAME, for *Coptodera variegata* Chaudoir.

Notes about nomenclature.-- *Coptodera variegata* Chaudoir (1869: 168) is a junior secondary homonym of *C. variegata* (Chaudoir 1848: 117) which was originally described as a *Stenoglossa*. According to the International Code of Zoological Nomenclature (Third Edition, Article 60), a replacement name must be provided. As a new name, we propose *Coptodera sallei*, in memory of Auguste Sallé, and in recognition of his many contributions to knowledge of Neotropical Carabidae.

Comparisons.-- Males of *C. versicolor* also exhibit a dense brush of setae on the ventral surface of the fore-femur (Fig. 8).

Description.-- Character states of the *C. sallei* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Dark ferrugineous to rufo-piceous with greenish to aeneous luster; elytra with testaceous to rufo-testaceous markings; lateral margins of elytra slightly paler; appendages brunneous to rufo-piceous; antennae and mouthparts rufo-testaceous to brunneous; palps with apices testaceous; labrum testaceous laterally towards base.

Mouthparts. Mandibles as in Figs. 2A-2F; maxilla as in Fig. 5.

Elytra (Fig. 14A). Interneurs impunctate.

Male genitalia (Figs. 14B-14C). Median lobe with apical portion medium-short, in lateral-left aspect trianguloid, in dorsal aspect sides parallel; apex narrowly rounded in lateral-left and dorsal aspect.

Notes about habitat.--Specimens were taken in México under bark at altitudes of 1219-1981m.

Geographical distribution (Map 1).-- This species is only known from the Pacific Versant of Guatemala and the Gulf Versant of México.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for the *C. sallei* group, above.

Material examined.-- We examined 40 specimens, including types, and saw non-type material from the following localities:

GUATEMALA Chimaltenango. Finca Monserrat, w slope V. Acatenango (FMNH); **Quezaltenango**. Cerro Zunil (BMNH)(MNHP).

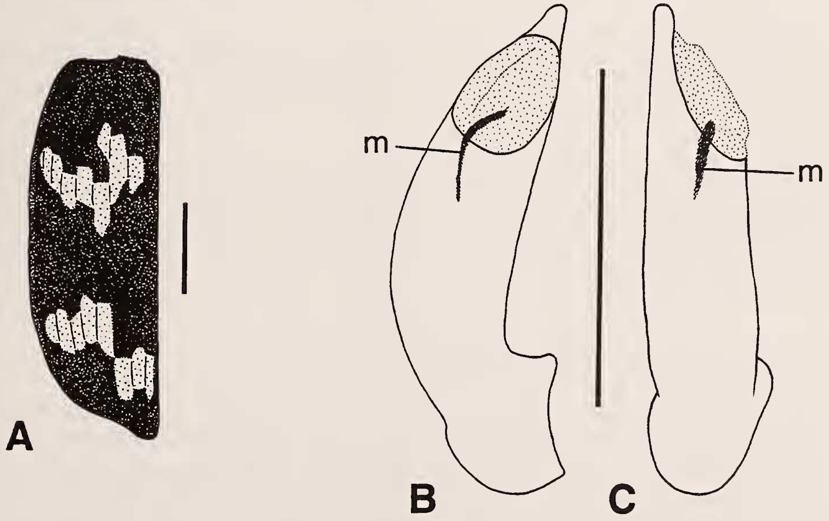
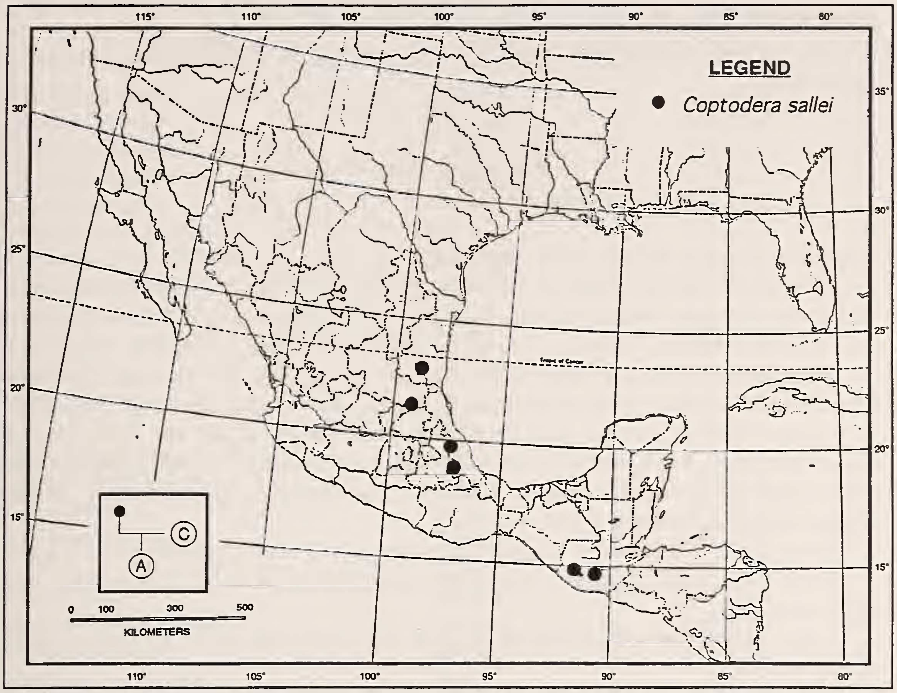


FIGURE 14. Line drawings of structures of *C. sallei*, new name. Fig. A: left elytron, dorsal aspect. Figs. B-C: male genitalia, left lateral and dorsal aspects respectively. Scale bars = 1 mm. Legend: m, microtrichial field.

TABLE III. Variation in SBL among females of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	5.67-6.92	6.27
C. elongata Putzeys	México	10	9.17-10.58	9.84
C. schaumi Chaudoir	Costa Rica	4	8.08-9.42	8.67
C. megalops Bates	Bolivia	8	6.25-8.92	7.90
C. championi Bates	Panamá	10	6.92-8.83	7.73
C. apicalis, new species	Colombia	3	8.25-10.50	9.61
	Ecuador	10	6.83-10.08	8.36
C. xanthopleura Bates	México	10	5.60-6.84	6.10
C. aurata Chevrolat	México	10	6.17-7.67	6.84
C. viridis, new species	Panamá	8	6.17-7.17	6.77
C. depressa Dejean	Brazil	10	6.33-8.50	7.53
C. versicolor Bates	Brazil	3	6.67-7.92	7.28
	Peru	3	6.92-7.50	7.17
C. dromioides Bates	Brazil	5	3.74-3.98	3.90
C. nigrosignata Chaudoir	Brazil	5	3.16-3.40	3.26
C. fulminans Bates	Brazil	2	3.42-3.48	3.45
C. nigrostriata Reiche	Bolivia	3	3.48-3.94	3.65
	Brazil	3	3.50-3.84	3.66
C. lineata Bates	México	10	3.00-3.36	3.20
C. stockwelli, new species	Panamá	10	3.20-3.74	3.50
C. transversa Reiche	México	10	3.06-3.50	3.21
C. squiresi Chaudoir	Brazil	1	4.72	4.72
C. sahlbergi Chaudoir	Brazil	4	5.58-6.88	6.01
C. relucens Bates	Brazil	2	5.48	5.48
C. pakitza, new species	Peru	2	6.00-6.16	6.08
C. festiva Dejean	México	10	4.44-6.16	5.22
C. foveolata, new species	México	1	6.12	6.12
C. nigroviridis, new species	México	1	5.28	5.28
C. rufescens Buquet	Brazil	1	9.42	9.42
C. aeneorufa Bates	Brazil	4	5.75-6.50	6.21
C. bifasciata Putzeys	Brazil	2	5.48-5.56	5.52
C. tripartita Chaudoir	Brazil	5	5.64-5.92	5.77
C. cupreotincta Bates	Panamá	10	6.17-7.33	6.68
C. braziliensis, new species	Brazil	2	6.00-7.17	6.59
C. chalcites Bates	Brazil	2	7.33-9.08	8.21
	Peru	2	6.58-7.42	7.00
C. acutipennis Buquet (see Table VIII)				
C. picea Dejean	México	10	4.32-5.24	4.83
C. nitidula Buquet	Ecuador	10	3.80-5.52	4.46
C. brunnea, new species	U.S.A.	10	5.60-6.28	6.06
C. aerata Dejean	U.S.A.	10	4.60-5.56	5.10
C. erwini, new species	Peru	1	4.36	4.36
C. tripunctata, new species	Peru	1	4.16	4.16



MAP 1. Geographical distribution of *Coptodera sallei*, new name. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

MÉXICO (BMNH)(IZWP); **Queretero**. 8.3 km w San Luis Potosí Queretero border, Hwy. 120 (SEMC); **Tamaulipas**. Mun. Gomez Farias, 2 km sw San Jose (TAMU); **Veracruz**. Cordova (BMNH); Jalapa (AMNH)(BMNH)(MCZ)(MNHP). Collections were made in March, May and July.

Coptodera elongata Group

This group has five species with character states as for *C. sallei* group, except the elytral apices of most species are spinose (Figs. 15B-E), the umbilical series of elytron with 16 or more setae, and the fore-femur of males lacks a dense brush of setae on the ventral surface. See Table I for features of mandibles. Male genitalia with median lobe left pleuropic-catopic, more catopic than pleuropic; membranous portion various, medium-short to short; internal sac without macrotrichia or macrospines (Figs. 16A-16J). Ovipositor with ensiform setae of stylomere 2 dorso-lateral (cf. Fig. 12A); nematiform setae absent. The geographical range of this group extends from the Amazon Basin in South America through Central America into México.

Chorological affinities.-- Geographical range overlaps broadly those of the *C. sallei* and *C. aurata* groups (Maps 1-5).

Phylogenetic relationships (Fig. 35).-- This group is the postulated adelphotaxon of the *C. aurata* group.

Coptodera elongata Putzeys
Figs. 13A, 15A, 16A & 16B; Map 2

Coptodera elongata Putzeys 1845: 395. Type material: LECTOTYPE (here selected) female, labelled: ex Musaeo Chaudoir (red print); Museum Paris ex Coll R. Oberthür (light green paper); elongata Putzeys Orizaba Guex & Sallé (original box label)[MNHP]. Type locality: Orizaba, Veracruz, Mexico.-- Chaudoir, 1869: 170.-- Bates 1883: 180.

Description.-- Character states of the *C. elongata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Rufo-piceous to piceous, with greenish luster; elytra with testaceous markings; appendages rufo-piceous; antennomeres 1-4 black, 5-11 brunneous to dark brunneous; mouthparts rufo-piceous; palpomeres with apices testaceous; and labrum testaceous laterally towards base. Ventral surface and femora faintly iridescent.

Fixed setae. Basal lateral setigerous puncture of pronotum in corner of hind angle.

Elytra (Fig. 15A). Interneurs impunctate; apex with lateral angle sharply obtuse and sutural angle rounded.

Legs. Fore-femur and mid-femur of male with numerous and fewer setae respectively on ventral surface.

Male genitalia. Median lobe as in Figs. 16A-16B, with membranous portion short; apical portion in lateral-left aspect short, trianguloid, tapered gradually to apex, in dorsal aspect broader; apex in lateral aspect acute, narrowly rounded, in dorsal aspect more broadly so.

Female genitalia. Reproductive tract as in Fig. 13A.

Notes about habitat.-- In México specimens were taken at altitudes of 30-1372 m; in bromeliads; on downed log with fungus; under bark; and at light. In Guatemala a specimen was taken at 1400-1500 m altitude on logs at night.

Geographical distribution (Map 2).-- The known range of this species extends from the Gulf Versant of México north of the Isthmus of Tehuantepec to Costa Rica, in Lower Central America.

Chorological affinities.-- The range of this species partly overlaps that of *C. schaumi*, but otherwise *C. elongata* is isolated geographically from the other species of the *C. elongata* group.

Phylogenetic relationships (Fig. 36).-- This species is the adelphotaxon of the other species in the *C. elongata* group.

Material examined.-- We examined 119 specimens, including types, and saw non-type material from the following localities:

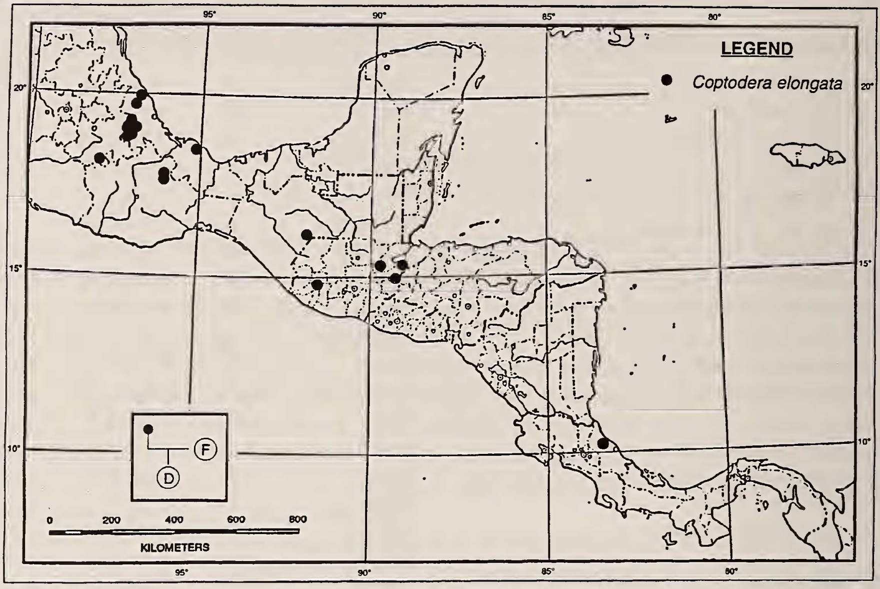
COSTA RICA Limón. Las Mercedes (MNHP).

GUATEMALA Alto Verapaz. Panzas (=Panzos?)(BMNH); Panzos (MCZ); **Izabel**. San Antonio, 10 km e La Francia (UGCG); **Quezaltenango**. Cerro Zunil (BMNH)(MNHP); **Zacapa**. Sierra del Espiritu Santo, 3 km se La Union (UASM).

MÉXICO (HNHM)(IZWP); **Chiapas**. Lagunas de Montebello Natl. Park, 4 km e Laguna Tziskaw at Dos Lagunas (CAS); **Oaxaca**. 9 km s Valle Nacional, Rte. 175 (UASM); 9.7 km s Valle Nacional (CNC); 12 km s Valle Nacional (CUIC); **Puebla**. Chinantla (BMNH); **Veracruz**. Cordoba (CAS)(UCBC); Fortin de las Flores (CAS)(CNC)(MCZ)(UASM)(UCBC); Jalapa(BMNH);

TABLE IV. Variation in Hw/Pw among males of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	0.81-0.88	0.84
C. elongata Putzeys	México	10	0.90-0.97	0.93
C. schaumi Chaudoir	Costa Rica	4	1.07-1.12	1.10
C. megalops Bates	Bolivia	10	1.06-1.11	1.09
C. championi Bates	Panamá	10	1.11-1.17	1.13
C. apicalis, new species	Colombia	4	1.14-1.21	1.17
	Ecuador	10	1.10-1.18	1.14
C. xanthopleura Bates	México	10	0.91-0.96	0.92
C. aurata Chevrolat	México	9	0.87-0.91	0.89
C. viridis, new species	Panamá	7	0.85-0.92	0.90
C. depressa Dejean	Brazil	10	0.88-0.94	0.91
C. versicolor Bates	Brazil	3	0.87-0.92	0.89
	Peru	3	0.87-0.90	0.89
C. dromioides Bates	Brazil	6	0.92-0.96	0.93
C. nigrosignata Chaudoir	Brazil	4	0.93-0.98	0.96
C. fulminans Bates	Brazil	2	0.93	0.93
C. nigrostriata Reiche	Bolivia	2	0.94-0.95	0.95
	Brazil	4	0.91-0.98	0.95
C. lineata Bates	México	10	0.93-1.00	0.97
C. stockwelli, new species	Panamá	10	0.93-0.95	0.94
C. transversa Reiche	México	10	0.95-1.00	0.98
C. sigillata, new species	Brazil	1	0.90	0.90
C. sahlbergi Chaudoir	Brazil	4	0.73-0.79	0.77
C. relucens Bates	Brazil	2	0.73	0.73
C. poecila Bates	Panamá	1	0.78	0.78
C. festiva Dejean	México	10	0.76-0.81	0.78
C. foveolata, new species	México	2	0.73-0.74	0.74
C. nigroviridis, new species	México	1	0.74	0.74
C. rufescens Buquet	Brazil	1	0.79	0.79
C. teutonica, new species	Brazil	1	0.76	0.76
C. aeneorufa Bates	Brazil	6	0.76-0.85	0.81
C. bifasciata Putzeys	Brazil	2	0.82-0.88	0.85
C. tripartita Chaudoir	Brazil	5	0.83-0.88	0.85
C. cupreotincta Bates	Panamá	10	0.76-0.83	0.79
C. braziliensis, new species	Brazil	4	0.79-0.86	0.82
C. chalcites Bates	Brazil	6	0.79-0.86	0.82
	Peru	8	0.79-0.84	0.82
C. emarginata Dejean	Brazil	5	0.71-0.76	0.73
C. acutipennis Buquet (see Table IX)				
C. picea Dejean	México	10	0.89-0.94	0.91
C. nitidula Buquet	Ecuador	10	0.89-0.94	0.91
C. brunnea, new species	U.S.A.	10	0.89-0.95	0.92
C. aerata Dejean	U.S.A.	10	0.86-0.93	0.89
C. waytkowskii Liebke	Brazil	3	0.88-0.94	0.90



MAP 2. Geographical distribution of *Coptodera elongata* Putzeys. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

Est. Biol. Los Tuxtlas (FSCA); Misantla (BMNH); Motzoronga (DEUN); Orizaba (MNHP); Rio Metlac, Fortin de las Flores (UCBC); Rio Metlac Cyn., nw Fortin de las Flores (UCBC); 4 km w Sontecomapan (UASM). Collections are recorded in all months of the year except November.

One specimen (IZWP) labelled "Peru?", which we believe is incorrect.

Coptodera schaumi Chaudoir
Figs. 15B, 16C & 16D; Map 3

Pericalus bifasciatus Schaum 1860: 191. Type material: not seen. Type area: Costa Rica.-- Chaudoir 1861: 123.

Coptodera bifasciata: Chaudoir 1861: 123.

Coptodera schaumi Chaudoir 1861: 123. Replacement name for *C. bifasciata* (Schaum) (*nec* Putzeys).-- 1869: 171.-- Bates 1883: 180.

Notes about type material.-- The type of *P. bifasciata* Schaum was not seen. Schaum's habitus illustration is diagnostic. In the MNHP is a male labelled: Pericalus bifasciatus Schaum (handwritten); Ex Musaeo Chaudoir (red print); TYPE (red paper); Schaumi Chaudoir Costa Rica Stevens (original box label); Museum Paris ex Coll R. Oberthür (light green paper). It is obvious from the labels on this specimen that Chaudoir had seen a specimen of the species for which he

TABLE V. Variation in Hw/Pw among females of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	0.82-0.88	0.85
C. elongata Putzeys	México	10	0.89-0.94	0.92
C. schaumi Chaudoir	Costa Rica	4	1.04-1.10	1.07
C. megalops Bates	Bolivia	8	1.04-1.14	1.09
C. championi Bates	Panamá	10	1.08-1.15	1.13
C. apicalis, new species	Colombia	3	1.09-1.17	1.12
	Ecuador	10	1.11-1.20	1.15
C. xanthopleura Bates	México	10	0.89-0.96	0.93
C. aurata Chevrolat	México	10	0.87-0.92	0.89
C. viridis, new species	Panamá	8	0.89-0.93	0.91
C. depressa Dejean	Brazil	10	0.89-0.94	0.91
C. versicolor Bates	Brazil	3	0.92-0.94	0.93
	Peru	3	0.86-0.90	0.88
C. dromioides Bates	Brazil	5	0.89-0.94	0.92
C. nigrosignata Chaudoir	Brazil	5	0.91-0.95	0.93
C. fulminans Bates	Brazil	2	0.91-0.92	0.92
C. nigrostriata Reiche	Bolivia	3	0.89-0.93	0.91
	Brazil	3	0.89-0.90	0.90
C. lineata Bates	México	10	0.93-0.98	0.96
C. stockwelli, new species	Panamá	10	0.91-0.96	0.93
C. transversa Reiche	México	10	0.95-0.98	0.97
C. squiresi Chaudoir	Brazil	1	0.85	0.85
C. sahlbergi Chaudoir	Brazil	4	0.75-0.77	0.76
C. relucens Bates	Brazil	2	0.76	0.76
C. pakitza, new species	Peru	2	0.78-0.81	0.80
C. festiva Dejean	México	10	0.77-0.84	0.80
C. foveolata, new species	México	1	0.71	0.71
C. nigroviridis, new species	México	1	0.74	0.74
C. rufescens Buquet	Brazil	1	0.84	0.84
C. aeneorufa Bates	Brazil	4	0.79-0.82	0.80
C. bifasciata Putzeys	Brazil	2	0.85-0.88	0.87
C. tripartita Chaudoir	Brazil	5	0.82-0.87	0.85
C. cupreotincta Bates	Panamá	10	0.76-0.83	0.79
C. braziliensis, new species	Brazil	2	0.81-0.85	0.83
C. chalcites Bates	Brazil	2	0.81	0.81
	Peru	2	0.80-0.82	0.81
C. acutipennis Buquet (see Table IX)				
C. picea Dejean	México	10	0.87-0.93	0.91
C. nitidula Buquet	Ecuador	10	0.88-0.97	0.92
C. brunnea, new species	U.S.A.	10	0.89-0.95	0.91
C. aerata Dejean	U.S.A.	10	0.88-0.94	0.92
C. erwini, new species	Peru	1	0.85	0.85
C. tripunctata, new species	Peru	1	0.88	0.88

provided a replacement name. However, this specimen cannot be the type of *P. bifasciata* Schaum as his specimen was collected by M. Wagner rather than by Stevens.

Description.-- Character states of the *C. elongata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum metallic green; elytra rufo-piceous to piceous with greenish to aeneous luster and testaceous markings; appendages, antennae, and mouthparts rufo-piceous; antennomeres 5-11 paler; palps with apices testaceous; labrum testaceous laterally towards base. Ventral surface and femora faintly metallic green.

Fixed setae. Basal lateral setigerous puncture of pronotum anterior of hind angle.

Elytra (Fig. 15B). Interneurs punctate; apex with lateral and sutural angles spinose.

Male genitalia. Median lobe as in Figs. 16C-16D, with membranous portion medium-short; apical portion short, in lateral aspect trapezoidal, in dorsal aspect trianguloid, tapered gradually to apex; apex in lateral aspect obliquely truncate, in dorsal aspect broadly rounded.

Notes about habitat.-- In Costa Rica, specimens were taken at altitudes of 500-700 m; under loose bark of *Enterolobium cyclocarpum* (Jacq.) Griseb. (eardrop tree). In Panamá, specimens were taken at light, both white and uv.

Geographical distribution (Map 3).-- The range of this species extends from the Amazon Basin of Brazil north through Lower Central America to Guatemala in Nuclear Central America.

Chorological affinities.-- The range of *C. schaumi* broadly overlaps that of *C. championi* and to a lesser amount that of *C. elongata*. The ranges of *C. schaumi*, *C. megalops*, and *C. apicalis* are in contact in a narrow zone in Northern South America (Maps 3 and 4).

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. megalops*.

Material examined.-- We examined 73 specimens, including types, and saw non-type material from the following localities:

BRAZIL Amazons (BMNH).

COLOMBIA Chocó. Marzo (MNHP); **?Santander/Boyaca**. Carare (MZSP); **Valle del Cauca/Caldas**. Santa Rosa, entre S. Francisco & Carthago (Etat de Cauca)[sic] (MNHP).

COSTA RICA (BMNH)(CAS)(IZWP)(MNHP)(ZSMM); **Alajuela**. Candelaria Tal. (BMNH); Cariblanco MSUC); **Cartago**. Juan Vinas (DEUN). Turrialba (CAS)(GRNC)(USNM); 3 km se Turrialba (UCBC); **Guanacaste**. Tilaran (OSUC); **Puntarenas**. 4 km n Tarcoles (CAS); **San Jose?**. Piedras Negras (UADE); ?. Chitaria (USNM). Collections were made in January, March, May, July, August and December.

GUATEMALA (BMNH).

NICARAGUA (BMNH)(MNHP); **Chontales**. (BMNH)(MNHP).

PANAMA Canal Zone. Albrook Forest Site, Fort Clayton (RTAC); Barro Colorado Isl. 9°10'N 79°50'W (USNM); **Chiriqui**. Tolé (BMNH); **Darien**. Santa Fe (OSUC); **Panamá**. Altos (Isla) de Maje 9°08'N 78°49'W (HPST); Bayano Dist., Majé Island (CAS). Collections were made in April to June.

Coptodera megalops Bates

Figs. 15C, 16E & 16F; Map 3

Coptodera megalops Bates 1869: 77. Type material: HOLOTYPE female, labelled: Ega; TYPE (red paper); megalops Bates (handwritten); Ex Musaeo H.W. Bates 1892; Paris Museum ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega, Amazonas, Brazil.

TABLE VI. Variation in Pw/Pl among males of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	1.71-1.93	1.86
C. elongata Putzeys	México	10	1.40-1.56	1.49
C. schaumi Chaudoir	Costa Rica	4	1.42-1.53	1.49
C. megalops Bates	Bolivia	10	1.50-1.58	1.54
C. championi Bates	Panamá	10	1.42-1.53	1.48
C. apicalis, new species	Colombia	4	1.43-1.59	1.49
	Ecuador	10	1.42-1.53	1.47
C. xanthopleura Bates	México	10	1.75-1.85	1.81
C. aurata Chevrolat	México	9	1.81-1.91	1.86
C. viridis, new species	Panamá	7	1.79-1.93	1.85
C. depressa Dejean	Brazil	10	1.69-1.89	1.75
C. versicolor Bates	Brazil	3	1.71-1.82	1.76
	Peru	3	1.72-1.76	1.75
C. dromioides Bates	Brazil	6	1.49-1.58	1.52
C. nigrosignata Chaudoir	Brazil	4	1.37-1.46	1.41
C. fulminans Bates	Brazil	2	1.42-1.43	1.43
C. nigrostriata Reiche	Bolivia	2	1.33-1.40	1.37
	Brazil	4	1.39-1.46	1.42
C. lineata Bates	México	10	1.38-1.50	1.44
C. stockwelli, new species	Panamá	10	1.34-1.44	1.38
C. transversa Reiche	México	10	1.41-1.54	1.47
C. sigillata, new species	Brazil	1	1.49	1.49
C. sahlbergi Chaudoir	Brazil	4	1.69-1.78	1.73
C. relucens Bates	Brazil	2	1.96	1.96
C. poecila Bates	Panamá	1	1.89	1.89
C. festiva Dejean	México	10	1.74-1.90	1.80
C. foveolata, new species	México	2	1.78-1.86	1.82
C. nigroviridis, new species	México	1	1.93	1.93
C. rufescens Buquet	Brazil	1	1.65	1.65
C. teutonica, new species	Brazil	1	1.75	1.75
C. aeneorufa Bates	Brazil	6	1.57-1.79	1.66
C. bifasciata Putzeys	Brazil	2	1.68-1.69	1.69
C. tripartita Chaudoir	Brazil	5	1.68-1.76	1.71
C. cupreotincta Bates	Panamá	10	1.64-1.79	1.72
C. braziliensis, new species	Brazil	4	1.57-1.67	1.62
C. chalcites Bates	Brazil	6	1.44-1.53	1.50
	Peru	8	1.50-1.64	1.55
C. emarginata Dejean	Brazil	5	1.62-1.78	1.71
C. acutipennis Buquet (see Table X)				
C. picea Dejean	México	10	1.60-1.68	1.65
C. nitidula Buquet	Ecuador	10	1.58-1.75	1.67
C. brunnea, new species	U.S.A.	10	1.54-1.67	1.59
C. aerata Dejean	U.S.A.	10	1.65-1.80	1.74
C. waytkowskii Liebke	Brazil	3	1.64-1.67	1.66

Coptodera batesi Chaudoir 1869: 172. Type material: LECTOTYPE (here selected) male, labelled: LECTO (red paper); TYPE (red paper); (green rectangle); Batesi Chaud (handwritten); Ex Musaeo Chaudoir (red print); megalops Bates Amazone Ega Bates (original box label); Coptodera megalops Bates det. George E. Ball '72; Paris Museum ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- Bates 1870: XVI.

Coptodera pertzeli Liebke 1951: 242. NEW SYNONYMY. Type material: PARATYPE female, labelled: Peru (handwritten); Sammlg. M. Liebke Eing. Nr. 56, 1932 (green paper); Erworben 1925 aus Sammlg. Oberndorffer Dr. Kallert; Kotype (pink paper); Coptodera pertzeli ♀ M. Liebke determ. Kotype; Inst. Zool. P.A.N. Warszawa 31/54 [IZWP]. Type area: Peru.

Coptodera peruana Liebke 1951: 243. NEW SYNONYMY. Type material: HOLOTYPE male, labelled: Peru (handwritten); Sammlg. M. Liebke Eing. Nr. 56, 1932 (green paper); Erworben 1925 aus Sammlg. Oberndorffer Dr. Kallert (upside down); TYPE (pink paper); Coptodera peruana Lbk. ♂ M. Liebke determ. Type; Inst. zool. P.A.N. Warszawa 31/54 [IZWP]. Type area: Peru.

Notes about synonymy.-- After examining the types of Liebke's species, we believe them to be conspecific with *C. megalops* Bates. Liebke based his two species on forms which had a slightly different elytral color pattern than in the type of *C. megalops*, but these differences are within the range of variation found in *C. megalops*.

Description.-- Character states of the *C. elongata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum metallic green; elytra rufo-piceous to black with greenish to aeneous luster and testaceous markings; appendages, antennae, and mouthparts rufo-piceous; antennomeres 5-11 paler; palps with apices testaceous; labrum testaceous laterally towards base. Ventral surface metallic green; femora faintly metallic green.

Fixed setae. Basal lateral setigerous puncture of pronotum anterior of hind angle.

Elytra (Fig. 15C). Interneurs punctate; apex with lateral and sutural angles spinose.

Male genitalia. Median lobe as in Figs. 16E-16F, with membranous portion medium-short; apical portion medium-short, in lateral aspect trianguloid, very slender, sloped abruptly, in dorsal aspect broader, irregular; apex in lateral aspect very slender, nearly pointed, in dorsal aspect irregular, and broadly rounded.

Notes about habitat.-- Specimens were taken at these altitudes in the following countries: 400-800 m in Bolivia; 430 m in Colombia; 100-250 m in Ecuador; and 290-1200 m in Peru. Specimens were taken under bark of fresh cut tree and in bark and frass in Ecuador; on logs in Peru.

Geographical distribution (Map 3).-- This species' range extends over the upper and middle part of the Amazon Basin in South America.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See topics for *C. schaumi* above, the adelphotaxon of *C. megalops*.

Material examined.-- A total of 174 specimens, including types, was examined. Non-type material was seen from the following localities:

BOLIVIA Cochabamba. Chapare-Gebiet, Oberer Rio Chipiriri (ZSMM); Region Chapare (BMNH)(ZSMM); Villa Tunari (UASM); **Santa Cruz**. (ZSMM). Not located "Ocobamba" (MNHP). Collections were made in February, April, May, August, and October.

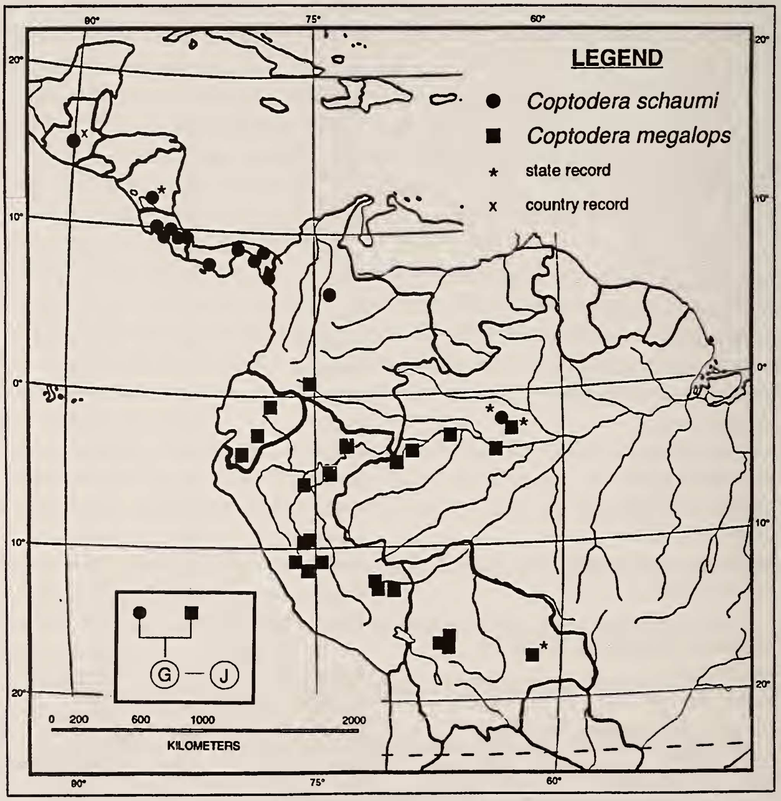
BRAZIL Amazons (BMNH); **Amazonas**. Benjamin Constant, Rio Javary (AMNH); Ega (BMNH)(MNHP); Fonte Boa (BMNH)(MNHP); S. Paulo de Olivença (CMNH). Collections were made in March to May.

TABLE VII. Variation in Pw/Pl among females of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	1.79-1.92	1.87
C. elongata Putzeys	México	10	1.45-1.54	1.51
C. schaumi Chaudoir	Costa Rica	4	1.50-1.53	1.52
C. megalops Bates	Bolivia	8	1.44-1.65	1.57
C. championi Bates	Panamá	10	1.40-1.60	1.49
C. apicalis, new species	Colombia	3	1.50-1.55	1.52
	Ecuador	10	1.43-1.57	1.51
C. xanthopleura Bates	México	10	1.76-1.86	1.81
C. aurata Chevrolat	México	10	1.75-1.94	1.86
C. viridis, new species	Panamá	8	1.73-1.92	1.80
C. depressa Dejean	Brazil	10	1.79-1.94	1.84
C. versicolor Bates	Brazil	3	1.72-1.75	1.73
	Peru	3	1.71-1.87	1.82
C. dromioides Bates	Brazil	5	1.51-1.57	1.53
C. nigrosignata Chaudoir	Brazil	5	1.39-1.44	1.42
C. fulminans Bates	Brazil	2	1.48	1.48
C. nigrostriata Reiche	Bolivia	3	1.44-1.50	1.46
	Brazil	3	1.44-1.49	1.46
C. lineata Bates	México	10	1.37-1.47	1.42
C. stockwelli, new species	Panamá	10	1.39-1.44	1.40
C. transversa Reiche	México	10	1.43-1.57	1.48
C. squiresi Chaudoir	Brazil	1	1.50	1.50
C. sahlbergi Chaudoir	Brazil	4	1.69-1.77	1.73
C. relucens Bates	Brazil	2	1.92	1.92
C. pakitza, new species	Peru	2	1.78-1.82	1.80
C. festiva Dejean	México	10	1.73-1.85	1.80
C. foveolata, new species	México	1	1.86	1.86
C. nigroviridis, new species	México	1	1.91	1.91
C. rufescens Buquet	Brazil	1	1.63	1.63
C. aeneorufa Bates	Brazil	4	1.62-1.71	1.68
C. bifasciata Putzeys	Brazil	2	1.60-1.71	1.66
C. tripartita Chaudoir	Brazil	5	1.63-1.73	1.68
C. cupreotincta Bates	Panamá	10	1.64-1.85	1.72
C. braziliensis, new species	Brazil	2	1.62-1.73	1.68
C. chalcites Bates	Brazil	2	1.55-1.63	1.59
	Peru	2	1.56-1.57	1.57
C. acutipennis Buquet (see Table X)				
C. picea Dejean	México	10	1.61-1.75	1.67
C. nitidula Buquet	Ecuador	10	1.61-1.72	1.64
C. brunnea, new species	U.S.A.	10	1.52-1.67	1.60
C. aerata Dejean	U.S.A.	10	1.67-1.79	1.71
C. erwini, new species	Peru	1	1.65	1.65
C. tripunctata, new species	Peru	1	1.74	1.75

COLOMBIA Caqueta. Morelia, Rio Bodoquero (USNM). Collection was made in January.
ECUADOR (BMNH); **Loja**. Loja (MNHP); **Napo Pastaza**. Limoncocha (CNC)(UASM); **Santiago-Zamora**. Macas (MNHP). Collections were made in April to August.
PERU (BMNH); **Huallaga**. Chambireyacù, nr. Yuirimaguas (MNHP); **Huánuco**. Bella Durmiente, nr Tingo Maria (UASM); Cueva de las Pavas Canyon, 8 km s Tingo Maria (FSCA); Monzon Valley, Tingo Maria (CAS); Pozuzo (HNHM)(MNHP); Tingo Maria (AMNH); 69.2 km e Tingo Maria (CAS); vic. Tingo Maria (UKLK); **Junín**. Chanchamayo (HNHM)(MCZ)(MNHP)(USNM); Sani Beni, 8 km e Satipo (SEMC); Satipo (AMNH)(CAS)(MCZ); **Loreto**. Pithecia, 74°05'S 05°02'W (USNM); Rio Napo, Explomapo Camp, Rio Sucusari, 03°15'S 72°55'W (USNM); **Madre de Dios**. Avispas (MCZ); 30 km sw P. Maldonado (USNM); Pakitza, 11°55'48"S 71°35'18"W (USNM); Pakitza, 12°07'S 70°58'W (USNM); Rio Tambopata Reserve, 30 air km sw of Puerto Maldonado (BMNH)(CAS); **Pasco?/Cuzco?**. Quiroz, Rio Paucartambo (MCZ). Not located "**Loreto**. Cavallo-Cocho" (MNHP). Collections were made in April to January.

One specimen labelled "Amazon, or Guatem." (BMNH).



MAP 3. Geographical distribution of *Coptodera schaumi* Chaudoir and *C. megaplops* Bates. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Coptodera championi Bates

Figs. 1C, 2G, 6A, 6E, 9A, 9B, 12A-12D, 15D, 16G & 16H; Map 4

Coptodera championi Bates 1883: 180. Type material: LECTOTYPE (here selected) female, one of a pair glued on same card, indicated by a small arrow, labelled: Type H.T. (disc with red border); Bugaba 800-1500' Champion; B.C.A. Col.I.1 Coptodera championi, Bates; Coptodera championi Bates (Bates' handwriting); LECTOTYPE ♀ Coptodera championi Bates By Erwin '76 [BMNH]. Type locality: Bugaba, Chiriqui Prov., Panamá.

Description.-- Character states of the *C. elongata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum metallic green; elytra rufo-piceous to piceous with greenish luster and testaceous markings; lateral margins of pronotum and elytra with cyaneous luster; appendages, antennae, and mouthparts rufo-piceous; terminal palpomeres with apices testaceous; labrum testaceous laterally towards base. Ventral surface and femora metallic blue.

Fixed setae. Basal lateral setigerous puncture of pronotum anterior of hind angle.

Mouthparts. Labrum as in Fig. 1C; left mandible as in Fig. 2G; labium as in Figs. 6A & 6E.

Elytra (Fig. 15D). Interneurs punctate; apex with lateral and sutural angles spinose.

Legs. Fore-tibia with long upper spur on inner surface (Fig. 9A); tarsal claws nearly smooth (Fig. 9B).

Male genitalia. Median lobe as in Figs 16G-16H, with membranous portion short; apical portion short, in lateral aspect broad, hardly tapered, in dorsal aspect similar, hardly tapered; apex in lateral aspect broadly rounded, in dorsal aspect sub-truncate.

Ovipositor. Stylomere 2 as in Figs. 12A-12D.

Notes about habitat.-- In Panamá this species has been taken at altitudes of 150-580 m, on logs, running on log, running on logs or branches at or near fermenting sap, at night, at white and uv lights.

Geographical distribution (Map 4).-- This species is known from Panamá and trans-Andean Colombia.

Chorological affinities.-- The ranges of *C. championi* and *C. apicalis* are adjacent to one another, and may meet in Colombia.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. apicalis*.

Material examined.-- A total of 128 specimens, including types were examined. Non-type material was seen from the following localities:

COLOMBIA Valle del Cauca. Buenaventura (BMNH); R. Dagua (MNHP).

PANAMA Bocas del Toro. 5 km sw Almirante 9°16'N 82°25'W (USNM); **Canal Zone**. Ciricito (USNM); Madden Forest, Mi 2, 9°05'N 79°37'W (DHK)(HPST); Barro Colorado Isl. 9°10'N 79°50'W (AMNH)(FMNH)(MCZ)(UCDC)(USNM); **Chiriqui**. (HNHM)(MNHP); Bugaba (MCZ)(MNHP)(UASM)(USNM); **Panamá**. Cerro Campana 8°40'N 79°56'W (USNM). Collections were made in January, and May to August.

Coptodera apicalis, new species

Figs. 7A, 15E, 16I & 16J; Map 4

Type material.-- HOLOTYPE male, labelled: ECUADOR:Esm.Pr. Zapallo Grande 4 February 1988 Mike Huybensz [USNM]. ALLOTYPE female, labelled same as holotype [USNM]. 43

additional PARATYPES, sex and label data as follows: 15 males and 11 females same as holotype [BMNH][CAS][FMNH][MNHP][QCAZ][UASM][USNM]. 3 males: ECUADOR Esmeraldas Pr. Zapallo Grande, Oct. 25-39, 1987 Michael Huybensz [CMNH]. 1 male: ECUADOR:Cotopaxi Guasaganda 500m 1 April 1988 Mike Huynesz [UASM]. 1 male: ECUADOR: Carchi Hojal VIII.9.1983 Coll. R. Davidson [CMNH]. 1 male and 2 females: ECUADOR: Carchi Hojal 25 July 1983 R.Davidson & J. Rawlins; running on moss & sheet fungus on large log [CMNH]. 2 females: SantoDomingo Ecuador2-X-50 JWFunkhouser; P. S. Bartholomew Collection Calif. Acad. Sci. Accession 1967 [CAS]. 1 male: 1200', Anchicaya Dam, 70 km E.Buenaventura, Valle,Colombia,VII.22, 1970. H. & A. Howden [UASM]. 1 female: 1200', Anchicaya Dam, 70 km E.Buenaventura, Valle,Colombia,VII.23, 1970. H. & A. Howden [UASM]. 1 male: COLOM.,1000' Anchicaya VII.21.1970 J.M. Campbell [CNC]. 2 females: COLOM.,1000' Anchicaya VII.22.1970 J.M. Campbell [CNC]. 2 males: COLOM.,1500' Anchicaya VII.26.1970 J.M. Campbell [CNC].

Type locality.-- Zapallo Grande, Esmeraldas province, Ecuador.

Derivation of specific epithet.-- From Latin *apex*, in allusion to the elongate pale apical markings on the elytra.

Description.-- Character states of the *C. elongata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum metallic green; elytra rufo-piceous to piceous with greenish to aeneous luster and testaceous markings; lateral margins of pronotum and elytra with cyaneous luster; appendages, antennae, and mouthparts rufo-piceous; terminal palpomeres with apices testaceous; labrum testaceous laterally towards base. Ventral surface and femora metallic blue.

Fixed setae. Basal lateral setigerous puncture of pronotum anterior of hind angle (Fig. 7A).

Elytra (Fig. 15E). Interneurs punctate; intervals 1-4 flat medially, convex in pale apical marking; apex with lateral and sutural angles spinose.

Legs. Tarsal claws nearly smooth.

Male genitalia. Median lobe as in Figs. 16I-16J, with membranous portion short; apical portion short, in lateral aspect broad, tapered slightly, in dorsal aspect similar, hardly tapered; apex in lateral and dorsal aspects broadly rounded.

Notes about habitat.-- Specimens were taken at altitudes of 304-457 m in Colombia and at 500 m in Ecuador; running on moss and sheet fungus on large logs in Ecuador.

Geographical distribution (Map 4).-- This species is known from the Chacó area of trans-Andean Colombia and Ecuador.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See topics for *C. championi* above, the adelphotaxon of *C. apicalis*.

Material examined.-- Type material only; see above for details.

Coptodera aurata Group

This group includes three species with character states of the *C. sallei* group, except the elytra are unicolorous rather than variegated, and the fore-femur of males lacks a dense brush of setae on the ventral surface. See Table I for features of mandibles. Male genitalia with median lobe left pleuropic-catopic, more catopic than pleuropic; membranous portion medium-short; internal sac without macrotrichia or macrospines (Figs. 17A-17F). Ovipositor with ensiform setae of stylomere 2 dorso-lateral (cf. Fig. 12A); nematiform setae present. The geographical range of this group is confined to Middle America, extending from México south to Nicaragua (Map 5).

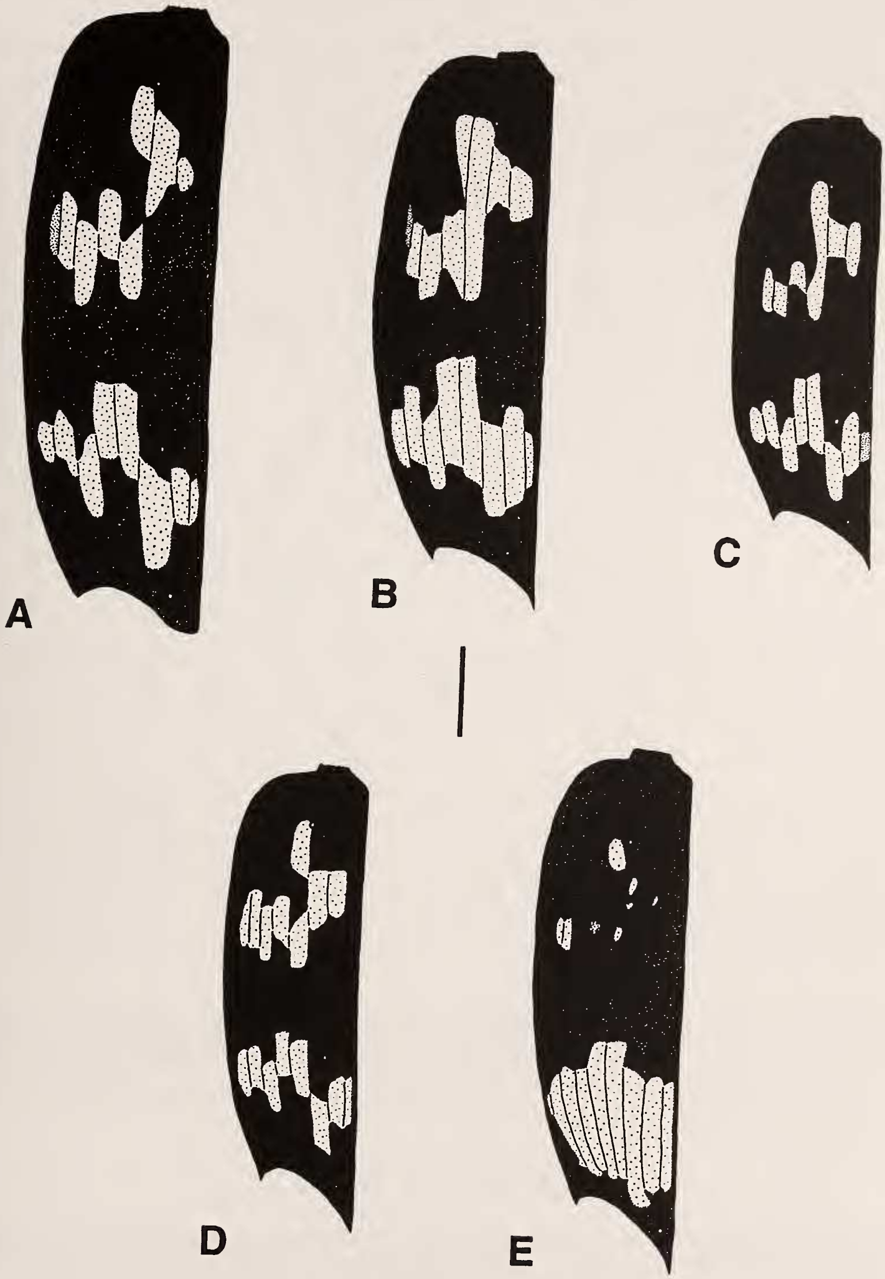


FIGURE 15. Line drawings of left elytron of *Coptodera elongata* group, dorsal aspect. Fig. A: *C. elongata* Putzeys. Fig. B: *C. schaumi* Chaudoir. Fig. C: *C. megalops* Bates. Fig. D: *C. championi* Bates. Fig. E: *C. apicalis*, new species. Scale bars = 1 mm.

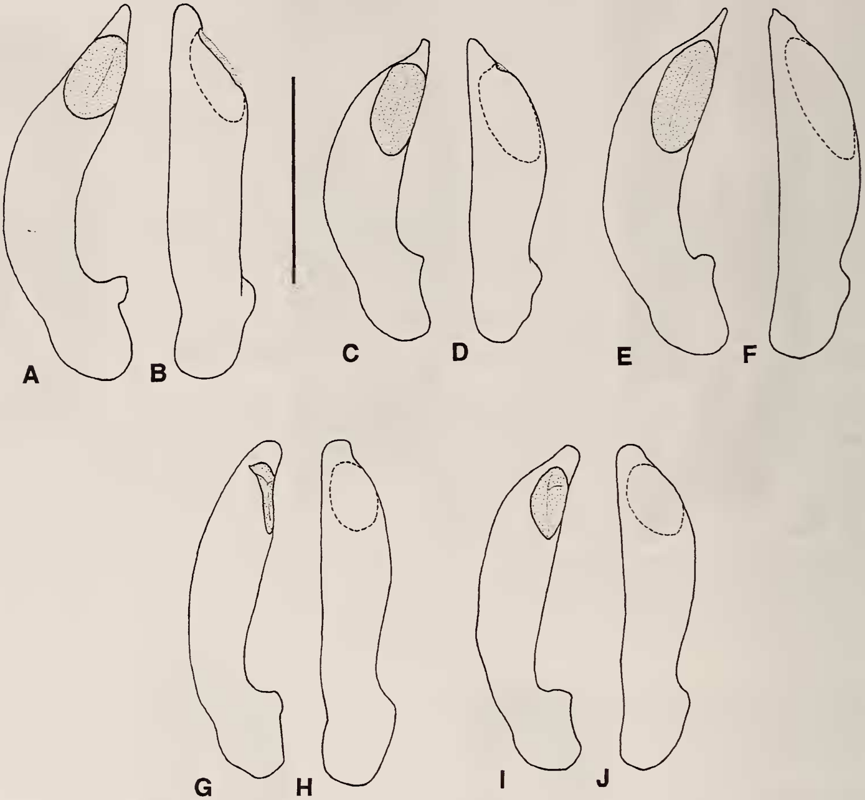
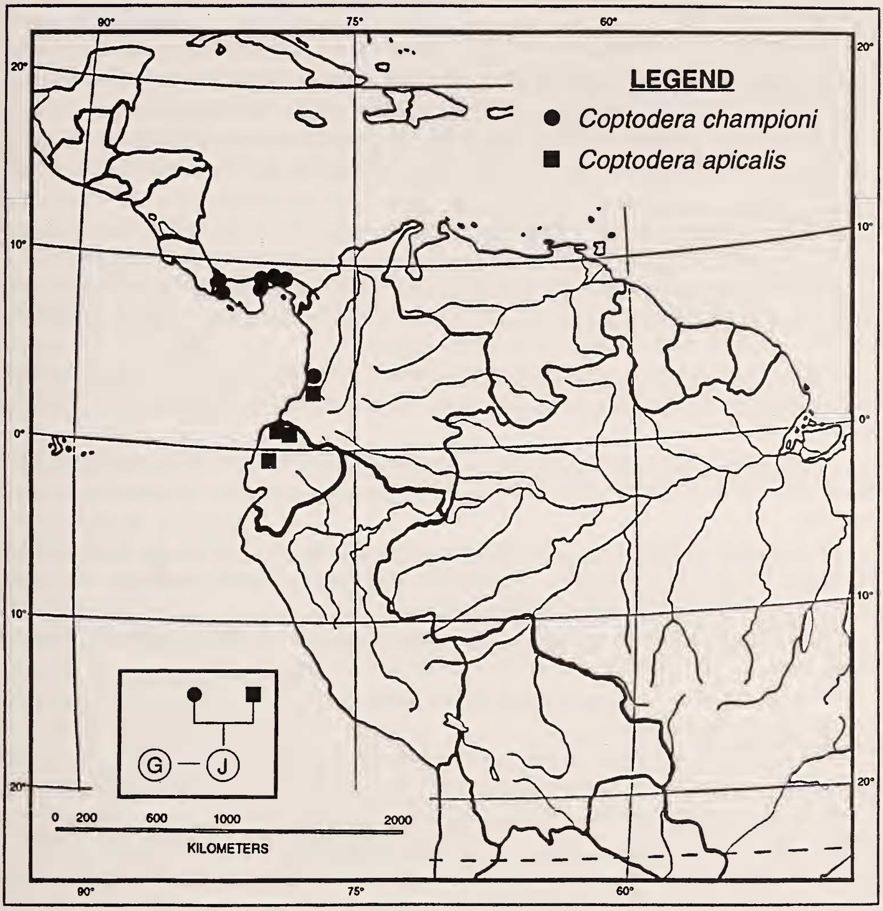


FIGURE 16. Line drawings of male genitalia of *Coptodera elongata* group. Figs. A, C, E, G & I left lateral aspect. Figs. B, D, F, H & J dorsal aspect. Fig. A-B: *C. elongata* Putzeys. Fig. C-D: *C. schaumi* Chaudoir. Fig. E-F: *C. megalops* Bates. Fig. G-H: *C. championi* Bates. Fig. I-J: *C. apicalis*, new species. Scale bars = 1 mm.

Chorological affinities.-- Geographical range of this group is overlapped broadly in Nuclear Middle America by those of the *C. sallei* and *C. elongata* groups (Maps 1-4).

Phylogenetic relationships (Fig. 35).-- This is the postulated adelphotaxon of the *C. elongata* group.



MAP 4. Geographical distribution of *Coptodera championi* Bates and *C. apicalis*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Coptodera xanthopleura Bates
Figs. 1D, 17A & 17B, Map 5

Coptodera xanthopleura Bates 1891: 270. Type material: LECTOTYPE (here selected) female, labelled: Type H.T. (disc with red border); Tehuantepec; Mexico Sallé Coll.; 1891-64; Coptodera xanthopleura Bates (Bates' handwriting) [BMNH]. Type locality: Tehuantepec, Oaxaca, México.

Notes about type material.-- In the MNHP is a female specimen labelled: Dos Arroyos Guerrero 1000 ft. Sept. H.H. Smith; Coptodera xanthopleura Bates (handwritten); Ex Musaeo H.W.

Bates 1892; Museum Paris ex Coll R. Oberthür (light green paper); and is here selected as PARALECTOTYPE.

Description.-- Character states of the *C. aurata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Elytra dark brunneous with faint greenish lustre; head and pronotum darker, faintly to brightly metallic green; lateral margins of elytra testaceous to rufo-testaceous; appendages, antennae, and mouthparts brunneous to dark brunneous; terminal palpomeres with apices testaceous.

Mouthparts. Labrum as in Fig. 1D.

Elytra. Interneurs impunctate.

Male genitalia. Median lobe as in Figs. 17A-17B, with apical portion short, in lateral-left aspect trianguloid, hardly tapered, in dorsal aspect broadly triangular; apex in lateral-left aspect narrowly rounded, more broadly so in dorsal aspect.

Notes about habitat.-- Specimens were taken at altitudes of 30-1500 m; at u-v light; in a tropical riparian forest; from a log in a thorn forest; and from under bark of a dead tree in a gallery forest.

Geographical distribution (Map 5).-- This species is known only from the Pacific Versant of México, from Nayarit (north of the Isthmus of Tehuantepec) to eastern Chiapas (in Nuclear Central America).

Chorological affinities.-- At its northern periphery, the range of *C. xanthopleura* is broadly overlapped by that of *C. viridis*. Southward, in Nuclear Central America, the range of *C. xanthopleura* is in contact with that of *C. aurata*.

Phylogenetic relationships (Fig. 36).-- As shown by genitalic features (Fig. 17), *C. xanthopleura* is the adelphotaxon of the species pair *C. aurata* + *viridis*.

Material examined.-- We examined 55 specimens, including types, and saw non-type material from the following localities:

MÉXICO(HNHM); **Chiapas**. Cinco Cerros, Km 30 on Hwy 190 (UASM); Cd. Cuauhtemoc (UASM); 4.7 & 7.9 km n Frontera Comalapa (UASM); Municipio La Trinitaria, 18 km s of La Trinitaria, small road nw Rte. 190 (CAS); **Jalisco**. nr Ixtapa (UASM); 2 km se Las Palmas (UASM); 33.8 km s Puerto Vallarata (UASM); **Nayarit**. 3 mi n Acaponeta (CDAE); Arroyo Canaveral, nr. Jesus Maria (CAS); Mecatan (AMNH); 9.2 km e San Blas, Rte. 46 (UASM); **Oaxaca**. 5 km e Tavela (UASM); **Sinaloa**. 6-7 km n La Capilla de Taxte (RHTC). Collections in May to July, September, and December.

Coptodera aurata Chevrolat
Figs. 17C & 17D; Map 5

Coptodera aurata Chevrolat 1835: No. 162. Type material: LECTOTYPE (here selected) labelled: (illegible handwritten label); Chevrolat Carabidae Fr. V. d. Poll. Pres. 1909 E.B. Poulton; TYPE COL: 125 1/2 Catascopus aurata Chevr. HOPE DEPT. OXFORD [HECO]. Type locality: near Las Vigas, Veracruz, México.-- Chaudoir 1869: 180.

Description.-- Character states of the *C. aurata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Dorsum metallic green to dark brunneous with greenish luster; lateral margins of elytra slightly paler; appendages brunneous to rufo-piceous; antennae testaceous to brunneous;

mouthparts brunneous to piceous; terminal palpomeres with apices testaceous; labrum testaceous laterally toward base.

Elytra. Interneurs punctate.

Male genitalia. Median lobe as in Figs. 17C-17D, with apical portion medium-short, in lateral-left aspect trianguloid, slender, narrow, in dorsal aspect broader, and irregular in outline; apex in lateral aspect narrowly rounded, in dorsal aspect more broadly so.

Notes about habitat.-- Specimens were taken in Guatemala at altitudes of 243-914 m and in México at 30-1219 m. Specimens were taken under bark in Guatemala, Honduras, México, and Nicaragua; beating live and dead vegetation, at uv light and in a tropical riparian forest in México.

Geographical distribution (Map 5).-- This species ranges in Nuclear Middle America from México on the Gulf Versant north of the Isthmus of Tehuantepec, southward to Nicaragua.

Chorological affinities.-- The range of this species is separated widely from that of its adelphotaxon, *C. viridis*.

Phylogenetic relationships (Fig. 36).-- *Coptodera aurata* and *C. viridis* are postulated to be adelphotaxa, as shown by similarities in form of the median lobe of the male genitalia (Figs. 17C-17F).

Material examined.-- A total of 130 specimens, including types, were examined. Non-type material was seen from the following localities:

EL SALVADOR (USNM).

GUATEMALA Escuintla. El Zapote (MNHP); Finca El Zapote, Zapote (FMNH); Mirandilla (BMNH); Pantaleon (BMNH)(MNHP)(USNM); **Quezaltenango**. El Reposo (BMNH)(MCZ)(USNM); Las Mercedes (BMNH)(MNHP); **San Marcos**. El Zumbador (="El Tumbador") (AMNH)(BMNH); **Suchitepéquez**. Cuyotenango, Finca San Rafael Olimpo (CNC) Collections in February and July.

HONDURAS Comayagua. Taladro (UCBC). Collection in January.

MÉXICO (BMNH)(CUIC)(HNHM); **Chiapas**. Cd. Cuauhtemoc (UASM); 7.9 km n Frontera Comalapa (UASM); 7 km w Rizo de Oro (UASM); 18.3 km s Solosuchiapa, Rte. 195 (UASM); Tapachula (BMNH); **Oaxaca**. Temascal (CAS); 9 km s Valle Nacional, Rte. 175 (UASM); **Puebla**. Puente Tepexco, nr Tepexco, Rte. 115 (UASM); 24.1 km e Tezuitlan (CNC); **Veracruz**. Almolonga (BMNH); Bobo (AMNH)(BMNH)(MCZ)(MNHP); Cordova (BMNH); Cosamatoapam (BMNH); Fortin de las Flores (OSUC); Coyame, Lake Catemaco (UASM); Jalapa (AMNH)(BMNH)(MNHP); Lake Catemaco (UASM); Playa Vicente (BMNH)(MNHP); Rio Metlac, Fortin de las Flores (UCBC); Rio Metlac Canyon, 4 km s Fortin (CUIC); 4 km w Sontecomapan (UASM). Collections in April to August.

NICARAGUA Esteli. 8 km n Esteli (CAS)(CNC). Collections in July.

Coptodera viridis, new species

Figs. 17E & 17F; Map 5

Type material.-- HOLOTYPE, male labelled: MEX. Jalisco nr. Ixtapa gallery forest, dead tree.ca.100' XII.22.70; Puerto Vallarta, MEX. trip, 1970 G.E. and K.E. Ball collectors [USNM]. ALLOTYPE, female labelled same as holotype [USNM]. 16 additional PARATYPES, sex and label data as follows: 7 males and 6 females same as holotype [BMNH][CNC][MCZ][MNHP] [UASM]. 1 female: MEX. Jalisco 2 kil.s.e.Las Palmas,ca.400' thorn forest, dead log XII.26.70; Puerto Vallarta, MEX. trip, 1970 G.E. and K.E. Ball collectors [UASM]. 1 female: Maria Madre Id. village May 14,1925; Tres Marias Islands; H.H.Keifer Collector [CAS]. 5 males and 2 females:

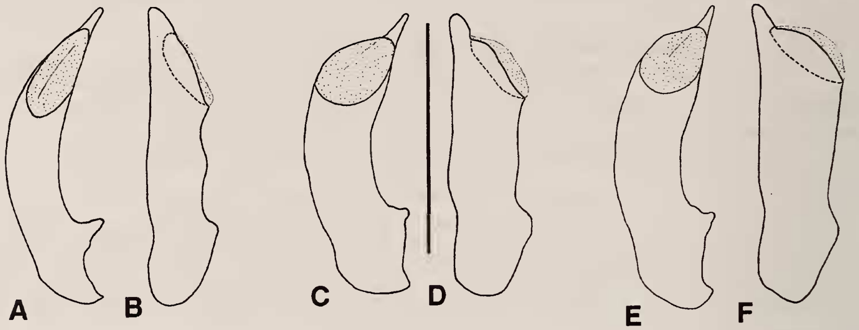
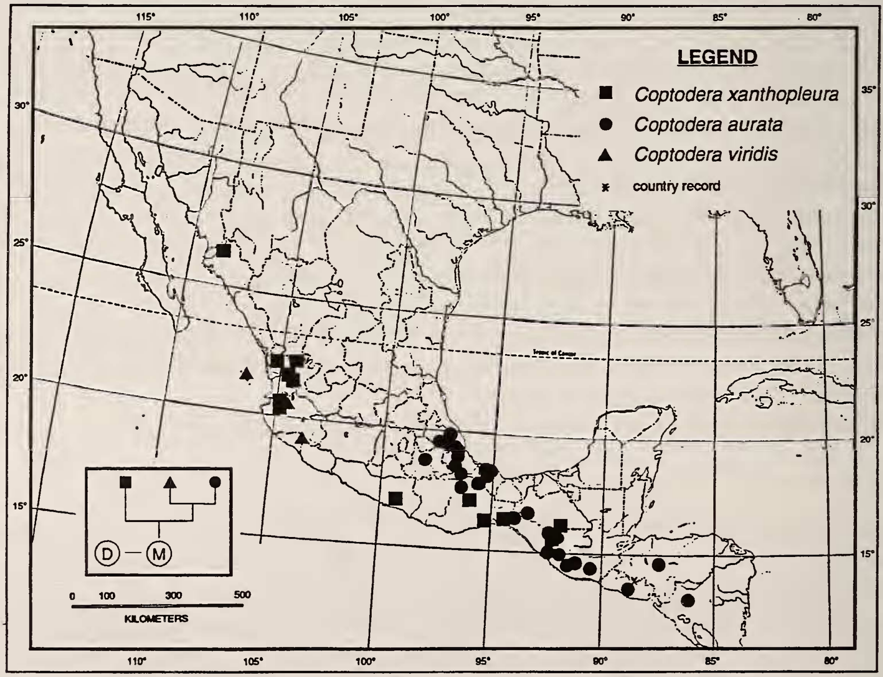


FIGURE 17. Line drawings of male genitalia of *Coptodera aurata* group. Figs. A, C & E left lateral aspect. Figs. B, D & F dorsal aspect. Figs. A-B: *C. xanthopleura* Bates. Figs. C-D: *C. aurata* Chevrolat. Figs. E-F: *C. viridis*, new species. Scale bars 1 mm.



MAP 5. Geographical distribution of *Coptodera xanthopleura* Bates, *C. aurata* Chevrolat and *C. viridis*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Maria Madre Id. village May 23,1925; Tres Marias Islands; H.H.Keifer Collector [CAS]. 1 female: MEXICO: 7 mi. NE. of Colima XII-3-1948; E.S. Ross Collector [CAS].

Type locality.-- Near Ixtapa, in the state of Colima, México.

Derivation of specific epithet.-- From the Latin adjective *viridis*, in allusion to the green color of this species.

Description.-- Character states of the *C. aurata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Dorsum metallic green to dark brunneous with greenish luster; lateral margins of elytra slightly paler; appendages brunneous; antennae and mouthparts dark testaceous to brunneous; palps with apices testaceous; labrum testaceous laterally towards base.

Elytra. Interneurs finely punctate.

Male genitalia. Median lobe as in Figs. 17E-17F; with apical portion short, in lateral-left aspect trianguloid, slender, narrow, in dorsal aspect trianguloid, broader; apex in left lateral aspect narrowly rounded, in dorsal aspect more broadly so.

Notes about habitat.-- This species has been taken at altitudes of 30-120 m; in gallery forest, thorn forest, from dead tree, and from a log.

Geographical distribution (Map 5).-- This species is known only from the Pacific Versant of southwestern México north of the Isthmus of Tehuantepec.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See topics for *C. aurata* above, the adelphotaxon of *C. viridis*.

Material examined.-- Type material only; see above for details.

Coptodera depressa Group

This group has two species which are characterized by a notched anterior margin of the labrum which is slightly wider than long, four discal setigerous punctures in the third interval on each elytron, elytra with variegated color pattern to unicolorous, markedly developed upper spur on the inner surface of the fore-femur, and mid-tibia of male notched on ventral surface near apex. See Table I for features of mandibles. Male genitalia with median lobe pleuropic-left; membranous portion elongate; internal sac without macrotrichia or macrospines (Figs. 19A-19D). Ovipositor with ensiform setae of stylomere 2 dorsal (cf. Fig. 12I); nematiform setae present. The geographical range (Map 6) of this group is northern and central South America, including the Amazon Basin and the Southern Atlantic zone.

Chorological affinities.-- The range of this group (Map 6) is broadly overlapped by most other groups of New World *Coptodera*.

Phylogenetic relationships (Fig. 35).-- This group is the adelphotaxon of the other groups of the 4-punctate lineage (lineage R, Fig. 35).

Coptodera depressa Dejean
Figs. 18A-18C, 19A & 19B; Map 6

Coptodera depressa Dejean 1831: 393. Type material: LECTOTYPE male, labelled: TYPE (red paper); depressa Klug in Brasilia (green paper); D. Klug (green paper); undulata Perty Mait:5; Ex Musaeo Chaudoir (red print); depressa Dejean Brésil Coll Dejean (original box label);

Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Brazil.-- Dejean & Boisduval 1829: 147.-- Chaudoir 1869: 166.

Coptodera undulata Perty 1830: 5, t. 1, f. 12. Type material: HOLOTYPE male, labelled: (green disc); Type.; undulata Perty (hand written); Holotypus Coptodera undulata Perty 1830 Zool. Staatssammlg. München (red paper) [ZSMM]. Type locality (here selected): Buenos Aires, state of Buenos Aires, Argentina.-- Chaudoir 1869: 166.

Coptodera plaumanni Liebke 1939: 127. NEW SYNONYMY. Type material: LECTOTYPE (here selected) male, labelled: (♂ on point supporting specimen); Chaco-Argentina Resistencia 2-1936- Col: M.VIANA (handwritten); Sammlung M. Liebke Hamburg; Kotype (pink paper); Coptodera plaumanni Lbk. M. Liebke determ. Kotype; Inst. Zool. P.A.N. Warszawa 31/54; Inst. Zool. P.A.N. Warszawa Cotypus Nr. 1351 (red paper) [IZWP]. Type locality: Resistencia, Argentina.

Notes about synonymy.-- The pale elytral markings of this species vary from markedly developed (Fig. 18A) to reduced (Figs. 18B & 18C) or completely lacking. Liebke based his description of *C. plaumanni* on six specimens which have reduced pale elytral markings. All these forms are conspecific. Based on examination of type material of the two named forms, we confirm the synonymy of *C. depressa* = *C. undulata.*

Description.-- Character states of the *C. depressa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum rufo-piceous, moderately metallic green to aeneous; elytra rufo-piceous, with greenish, aeneous, or faint purpureous lustre and testaceous to rufo-testaceous markings or without pale markings (unicolorous); lateral margin of elytra rufo-testaceous; appendages, antennae, and mouthparts rufo-testaceous to rufo-brunneous. Ventral surface rufo-brunneous.

Elytra (Figs. 18A-18C). Interneurs finely punctulate to impunctate.

Legs. The fore-femur of the male lacks the dense brush of setae from the ventral surface as seen in *C. versicolor.*

Male genitalia. Median lobe as in Figs. 19A-19B, with apical portion in lateral-left aspect moderately long, trianguloid, tapered gradually to apex, in dorsal aspect with sides parallel; apical portion in line with sagittal plane of median lobe; apex in lateral-left aspect acute, almost pointed, in dorsal aspect broadly rounded.

Notes about variation.-- The pale elytral markings vary from markedly developed to completely lacking (Figs. 18A-18C).

Notes about habitat.-- Adults were taken on trees and logs at night and on a logpile at night in a forest in Argentina.

Geographical distribution (Map 6).-- The range of this species appears to be in southeastern and central South America including the Southern Atlantic zone and Amazon Basin, and probably along the northern coast of South America to Colombia.

Chorological affinities.-- The range of *C. depressa* probably overlaps that of *C. versicolor* in the western part of the Amazon Basin (Map 6).

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. versicolor.*

Material examined.-- A total of 182 specimens, including types, were examined. Non-type material was seen from the following localities:

ARGENTINA La Pampa (Pico) (MCZ); **Chaco**. Resitencia (IZWP). **Misiones** bords du Rio Iguazu, chutes de l'Iguazu (MNHP); Iguazu Nat. Park (CMNC); 20 km s.e., Iguazu (CMNC); Jardin America, Salto Tabay (CMNC). Collections were made in July and December to February.

BRAZIL (BMNH)(FMNH)(IZWP)(MCZ)(MNHP)(ZSMM); **Bahia.** (BMNH)(MNHP); **Espirito Santo.** Esp. Santo (HNHM); Espirito Santo (BMNH)(UASM); **Goiás.** (MNHP); Corumba, Fazenda Monjolinho (MZSP); Jatahy (MNHP); Rio Verde (MNHP); **Minas Gerais.** Mar de Hespanha (BMNH); **Parana.** Rondon (MCZ); **Rio de Janeiro** Rio Jan. (BMNH)(CMNH)(MNHP); **Rio Grande do Sul.** (MCZ)(MNHP); Rio Grande (BMNH); **Santa Catarina.** (MCZ)(MNHP); Corupa (Hansa Humboldt) (AMNH)(MCZ); Hansa Humboldt (MNHP); Nova Teutonia (AMNH)(CAS)(MCZ)(UASM)(USNM)(ZSMM); **São Paulo.** (MNHP); Cerqueira Cesar (MNHP); Rio Piracicaba (MNHP); São Paulo (BMNH)(IZWP); Val. du Rio Pardo (MNHP). Not located "Boa Sorta" (BMNH)(MNHP). Collections were made throughout the year.

COLOMBIA (BMNH).

PARAGUAY Alto Parana. Puerto P. Stroessner (HNHM); 27 km w Pto. Pres. Stroessner (EGRC); **Concepción.** vic. Horqueta (MCZ); **Itapúa.** Hohenau (UASM). Collections were made in January and June.

TRINIDAD (UASM). Collection in July.

Coptodera versicolor Bates
Figs. 2H, 8C, 8D, 18D, 19C & 19D; Map 6

Coptodera versicolor Bates 1869: 76. Type material: LECTOTYPE (here selected) female, labelled: Ega; versicolor Bates; affinis Chd; ex Musaeo H.W. Bates 1892 Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.

Coptodera affinis Chaudoir 1869: 168. Type material: LECTOTYPE (here selected) male, labelled: TYPE (red paper); affinis Chaud (handwritten); Ex Musaeo Chaudoir (red print); versicolor Bates Amazone Bates (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- Bates 1870: XVI.

Notes about type material.-- Chaudoir's description was based on "two female specimens from Ega". The Chaudoir material in the MNHP consisted of two specimens, a male and a female. We assume that Chaudoir must have misidentified the sex of one of the specimens.

Comparisons.-- Males of *C. sallei* also exhibit a dense brush of setae on the ventral surface of the fore-femur.

Description.-- Character states of the *C. depressa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum rufo-piceous, moderately to brilliantly metallic green to aeneous; elytra rufo-piceous with greenish lustre basally and testaceous to rufo-testaceous markings, some specimens with overall aeneous lustre; lateral margin of elytra rufo-testaceous; appendages, antennae, and mouthparts testaceous to rufo-testaceous. Ventral surface rufo-brunneous.

Mouthparts. Left mandible as in Fig. 2H.

Elytra (Fig. 18D). Interneurs punctate.

Legs. Fore-femur of male with ventral brush of setae (Figs. 8C-8D).

Male genitalia. Median lobe as in Figs. 19C-19D, with apical portion flattened, in lateral-left aspect moderately long, trianguloid, tapered gradually to apex, in dorsal aspect trianguloid, gradually sloped to apex; apical portion slightly to right of sagittal plane of median lobe; apex in lateral-left aspect acute, almost pointed, in dorsal aspect broadly rounded.

Notes about habitat.-- Specimens were taken in the following countries at these altitudes: Bolivia at 400 m; Colombia at 213 m; Ecuador at 100 m; Peru at 290 m; and Venezuela at 140 m. Specimens were taken under bark of fresh cut tree in Ecuador; on logs, at uv light, and in subtropical rainforest in Peru; and under bark of cut timber with bracket fungi in a rainforest in Venezuela.

Geographical distribution (Map 6).-- The range of this species is extensive in the Amazon Basin of cis-Andean South America.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for *C. depressa* above, the adelphotaxon of *C. versicolor*.

Material examined.-- We examined 58 specimens, including types, and saw non-type material from the following localities:

BOLIVIA Cochabamba. (MNHP); Chaparé region (ZSMM); **Santa Cruz**. Valle Grande (MNHP). Collections were made in August to October, December, and February.

BRAZIL (MNHP); Amazon (BMNH); **Amazonas**. Ega (BMNH)(MNHP); Fonte Boa (MNHP); Sto. [sic] Paulo d'Olivença (MNHP); **Mato Grosso** Utiariti (MZSP); **Para**. (BMNH)(CMNH) (MNHP); Santarem (CMNH). Collections were made in June and July.

COLOMBIA Amazonas. Leticia (CNC)(UASM). Collection was made in July.

ECUADOR Napo Pastaza. Limoncocha (UASM); **Santiago-Zamora**. Macas (BMNH). Collection was made in April.

PERU Huallaga. (MNHP); Chambireyacu, nr. Yurimaguas (MNHP); Huánuco. Monzon Valley, Tingo Maria (CAS); **Loreto**. Rio Ampiyacu (FMNH); **Madre de Dios**. Manu National Park (CAS); Pakitza, 11°55'48"S 71°35'19"W (USNM); Pakitza, 12°07'S 70°58'W (USNM); Rio Tambopata Res., 30 km (air) sw Pto. Maldonato, 12°50'S69°20'W (BMNH)(USNM). Not located "**Loreto**. Cavallo-Cocho" (MNHP). Collections were made in May to December.

VENEZUELA Amazonas. Cerro de Neblina basecamp 0°50'N 66°10'W (USNM). Collection was made in February.

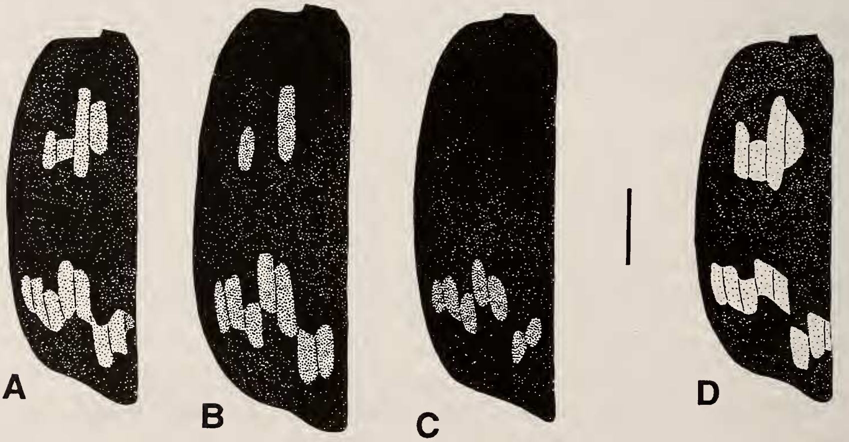
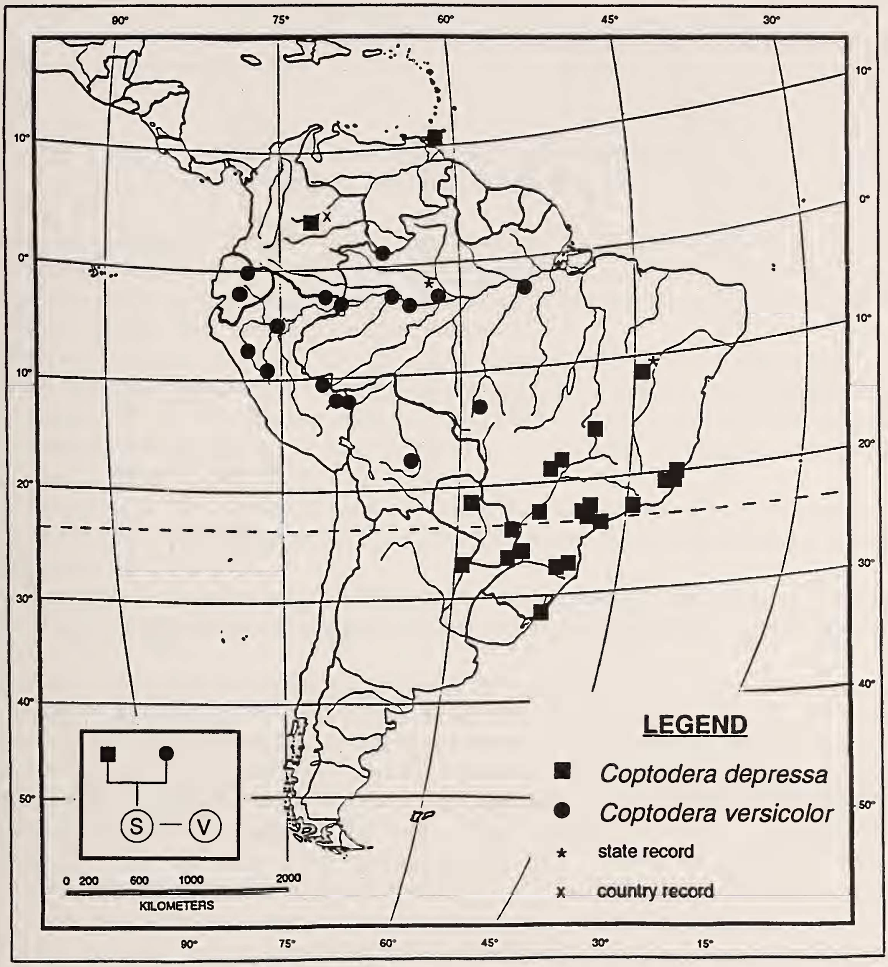


FIGURE 18. Line drawings of left elytron of *Coptodera depressa* group, dorsal aspect. Figs. A-C: *C. depressa* Dejean. Fig. D: *C. versicolor* Bates. Scale bars = 1 mm.



MAP 6. Geographical distribution of *Coptodera depressa* Dejean and *C. versicolor* Bates. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

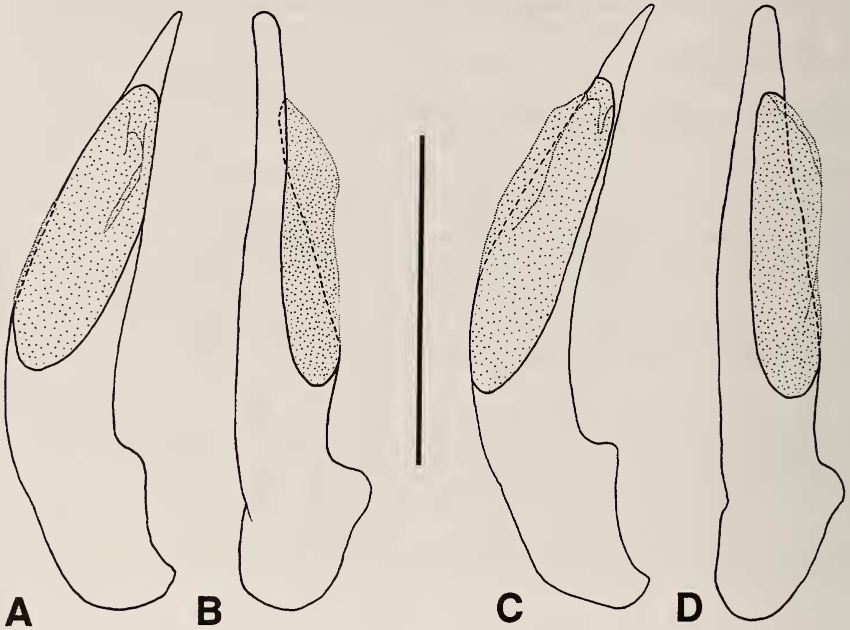


FIGURE 19. Line drawings of male genitalia of *Coptodera depressa* group. Figs. A & C left lateral aspect. Figs. B & D dorsal aspect. Figs. A-B: *C. depressa* Dejean. Figs. C-D: *C. versicolor* Bates. Scale bars = 1 mm.

Coptodera transversa Group

This group has nine species which are characterized by a shallowly emarginate anterior margin of labrum which is longer than wide, base of pronotum slightly to distinctly lobed medially, three or four discal setigerous punctures on each elytron, interneurs finely punctulate, elytra with variegated color pattern, markedly reduced or markedly developed upper spur on inner surface of the fore-tibia, and mid-tibia of male with notch on ventral surface near apex. See Table I for features of mandibles. Male genitalia with median lobe pleuropic-left; membranous portion short; internal sac without macrotrichia or macrospines (Figs. 21A-21P and 22A-22B). Ovipositor with ensiform setae of stylomere 2 dorsal (Fig. 12E); nematiform setae present. The geographical range of this group is extensive, from the Southern Atlantic zone of Brazil, through cis-Andean Colombia and north through Lower and Nuclear Central America to the Gulf and Pacific Versants of México north to the Isthmus of Tehuantepec.

Chorological affinities.-- The geographical range of the *C. transversa* group is broadly overlapped by most other groups of New World *Coptodera*.

Phylogenetic relationships (Fig. 36).-- This group is the postulated adelphotaxon of the *C. festiva* - *C. aerata* group lineage.

Coptodera dromioides (Bates), new combination
Figs. 20A, 21A & 21B; Map 7

Stenoglossa dromioides Bates 1869: 79. Type material: LECTOTYPE (here selected) female, labelled: Ega; dromioides Bates corticalis Chaud; ex Musaeo H.W. Bates 1892; LECTO TYPE (disc); LECTOTYPE Stenoglossa dromioides Bts det. George E. Ball 72 [MNHP]. Type locality: Ega, state of Amazonas, Brazil.

Stenoglossa corticalis Chaudoir 1869: 207. Type material: LECTOTYPE (here selected) male, labelled: Salhberg jun (hand written); corticalis Chaud (hand written); Brésil Cantagallo (hand written); Ex Musaeo Chaudoir (red print); LECTO TYPE (disc); LECTOTYPE Stenoglossa corticalis Chd det. George E. Ball 72 [MNHP]. Type locality: Cantagallo, state of Rio de Janeiro, Brazil.-- Bates 1870: XVII.

Recognition.-- This species is readily separated from other species of the *C. transversa* group on a combination of the following two characters: isodiametric elytral microsculpture and elytral color pattern.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head rufo-brunneous to brunneous; pronotum bicolored, rufo-brunneous to dark brunneous, with narrow testaceous anterior and posterior margins; elytra rufo-brunneous to nearly piceous with testaceous markings; appendages, antennae and mouthparts testaceous to brunneo-testaceous; ventral surface moderately to broadly testaceous along mid-line longitudinally, darkened to dark brunneous laterally, sternum 6 not pale medially; proepipleuron slightly paler or not; elytral epipleuron testaceous to brunneo-testaceous.

Fixed setae. Each elytron with four discal setae.

Elytra (Fig. 20A). Apical margin nearly straight; lateral margin hardly explanate in females.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

Male genitalia. Median lobe as in Figs. 21A-21B, with apical portion in lateral-left aspect medium-short, rod-like, slightly tapered, in dorsal, aspect slender, rod-like with parallel sides; apex in lateral-left and dorsal aspects narrowly rounded.

Notes about habitat.-- Specimens were taken at 300-500 m in Brazil and at 840 m in Peru.

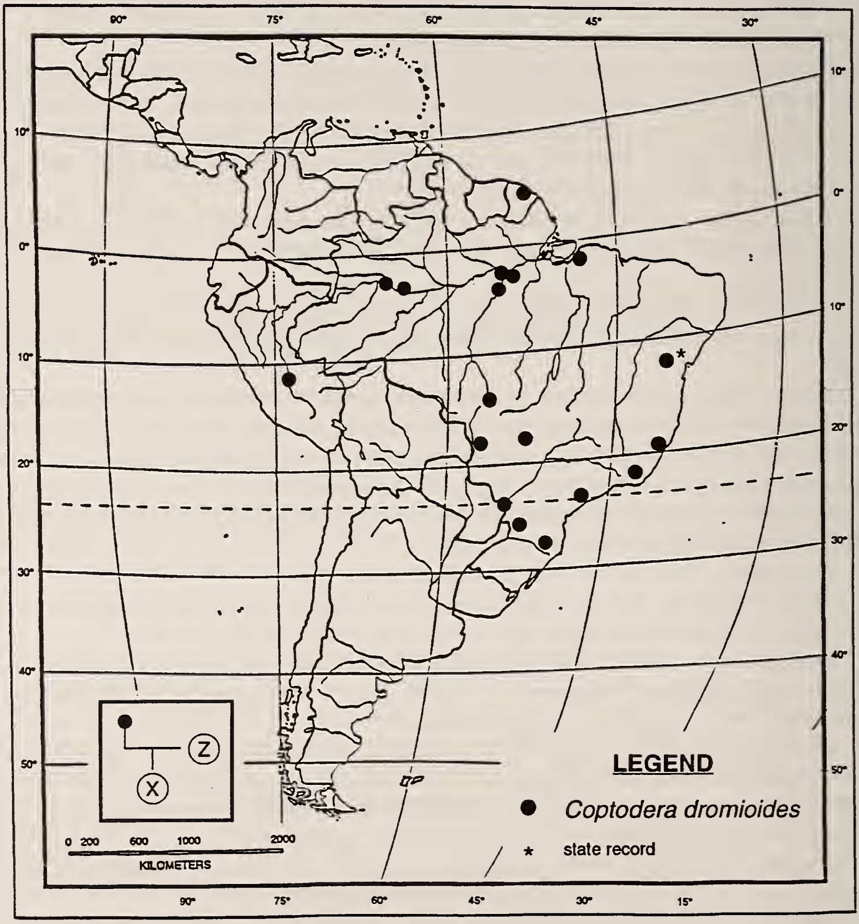
Geographical distribution (Map 7).-- This species is known only from Brazil (Southern Atlantic zone and Amazon Basin), French Guiana in northeastern South America, Paraguay, and cis-Andean Peru, to the west.

Chorological affinities.-- The geographical range of this species is overlapped broadly by the ranges of the other species in the *C. transversa* group (Maps 8-10).

Phylogenetic relationships.-- This species is the adelphotaxon of the remaining species in the *C. transversa* group.

Material examined.-- We examined 62 specimens, including types, and saw non-type material from the following localities:

BRAZIL Amazon (MNHP); **Amazonas** Ega (MNHP); Fonte Boa (MNHP); Itaituba (MNHP); Teffe (MNHP); **Bahia**. (MNHP); **Espirito Santo**. Esp. Santo (HNHM); **Goias**. Jatahy (MNHP); **Mato Grosso**. (MNHP); Chapada (CMNH); Corumba (CMNH); **Para**. (BMNH); Pará (MCSN); Santarem (BMNH)(CMNH); Tapajos (MNHP); **Rio de Janeiro** N. Friborg (MNHP); **Santa Catarina**. Nova Teutonia (USNM); São **Paulo**. Piracicaba (UASM); São Paulo (BMNH)(MNHP); Val du Rio Pardo (MNHP). Collections in October to December.
FRENCH GUIANA Cayenne (MNHP).
PARAGUAY Alto Parana. Puerto P. Stroessner (HNHM). Collection in December.
PERU Junín. Sani Beni, 8 km e Satipo (SEMC). Collection in November.



MAP 7. Geographical distribution of *Coptodera dromioides* (Bates). Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

Coptodera nigrosignata (Chaudoir), new combination
Figs. 20B, 21C & 21D; Map 8

Stenoglossa nigrosignata Chaudoir 1869: 206. Type material: LECTOTYPE (here selected) female, labelled: Ex Musaeo Chaudoir (red print); LECTO TYPE (disc); LECTOTYPE Stenoglossa nigrosignata Chd det. George E. Ball 72; fulminans Bates Amazone Ega Bates (handwritten box label); MUSEUM PARIS 1952 COLL R. OBERTHUR (light green paper) [MNHP]. Type locality: Ega, state of Amazonas, Brazil.

Recognition.-- This species is readily separated from other species of the *C. transversa* group on the combination of two characters: isodiametric elytral microsculpture and elytral color pattern.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum testaceous to brunneo-testaceous; elytra testaceous to brunneo-testaceous with rufo-brunneous to dark brunneous markings; appendages, antennae and mouthparts testaceous; ventral surface broadly testaceous along mid-line longitudinally, abdominal sterna darkened slightly laterally, sternum 6 with apical margin paler, remainder of ventral surface darkened to brunneous laterally; proepipleuron and elytral epipleuron testaceous to brunneo-testaceous.

Fixed setae. Each elytron with four discal setae.

Elytra (Fig. 20B). Apical margin nearly straight; lateral margin slight explanate in females.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

Male genitalia. Median lobe as in Figs. 21C-21D, with apical portion in lateral-left aspect short, trianguloid, tapered gradually to apex, in dorsal aspect tapered gradually, abruptly widened at apex; apex in lateral-left aspect narrowly rounded, in dorsal aspect obliquely truncate.

Notes about habitat.-- None available.

Geographical distribution (Map 8).-- This species in known only from the Amazon Basin of Brazil.

Chorological affinities.-- The range of this species is isolated from that of the related *C. fulminans*, but is overlapped broadly by the range of another relative, *C. nigrostriata*.

Phylogenetic relationships (Fig. 36).-- This species is part of a trichotomy with *C. fulminans* and the *C. nigrostriata* - *C. stockwelli* lineage.

Material examined.-- We examined 12 specimens, including types, and saw non-type material from the following localities:

BRAZIL Amazonas. Fonteboa (MNHP); Maturacá, Rio Negro (MPEG); **Mato Grosso**. (MNHP); Sinop (CMNH); **Para**. (CMNH).Collections in October and January.

Coptodera fulminans (Bates), new combination
Figs. 20C, 21E & 21F; Map 8

Stenoglossa fulminans Bates 1869: 78. Type material: HOLOTYPE female, glued on card, labelled: fulminans Bates Bahia (hand written); nigrosignatus Chaud? (hand written); Ex Musaeo H.W. Bates 1892; HOLOTYPE Stenoglossa fulminans Bts det. George E. Ball 72 [MNHP]. Type area: state of Bahia, Brazil.

Stenoglossa nigrosignata: Bates 1870: XVII (not Chaudoir).

Note about synonymy.-- Bates (1870: XVII) misinterpreted Chaudoir's *C. nigrosignata*, as shown by study of type material.

Recognition.-- This species is readily separated from the other species of the *C. transversa* group on a combination of two characters: isodiametric elytral microsculpture and elytral color pattern.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum testaceous to brunneo-testaceous; elytra testaceous to brunneo-testaceous with rufo-brunneous to brunneous markings; appendages, antennae and mouthparts testaceous; ventral surface broadly testaceous along mid-line longitudinally, darkened to brunneous laterally, sternum 6 brunneo-testaceous to rufo-brunneous with apical margin paler; proepipleuron and elytral epipleuron testaceous.

Fixed setae. Each elytron with four discal setae.

Elytra (Fig. 20C). Apical margin nearly straight; lateral margin slightly explanate in females.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

Male genitalia. Median lobe as in Figs. 21E-21F, with apical portion in lateral-left aspect medium-short, slender, tapered gradually, the parallel-sided, curved dorsally, in dorsal aspect sides gradually tapered to apex; apex in lateral-left and dorsal aspects narrowly rounded.

Notes about habitat.-- One specimen was taken at 30 m in Brazil.

Geographical distribution (Map 8).-- This species is known only from the Southern Atlantic zone of Brazil.

Chorological affinities.-- The geographical range of this species is isolated from the ranges of *C. nigrosignata*, *C. nigrostriata*, *C. lineata* and *C. stockwelli*.

Phylogenetic relationships (Fig. 36).-- See topic for *C. nigrosignata* above.

Material examined.-- We examined 4 specimens, including the type, and saw non-type material from the following localities:

BRAZIL Minas Gerais. Caraça (MNHP); **Paraiba**. Joao Pessoa, forest of Buranquinho (CMNH); **Santa Catarina**. Nova Teutonia (CAS). Collections in January and July.

Coptodera nigrostriata (Reiche), new combination

Figs. 10A, 20D, 21G & 21H; Map 9

Tetragonoderus nigrostriatus Reiche 1843: 179. Type material: HOLOTYPE female, labelled: Tetragonoderus nigrostriatus Reiche Venezuela (hand written); Ex Musaeo Chaudoir (red print); HOLOTYPE Stenoglossa nigrostriata Reiche det. George E. Ball 72 [MNHP]. Type locality: near Caracas, Venezuela.

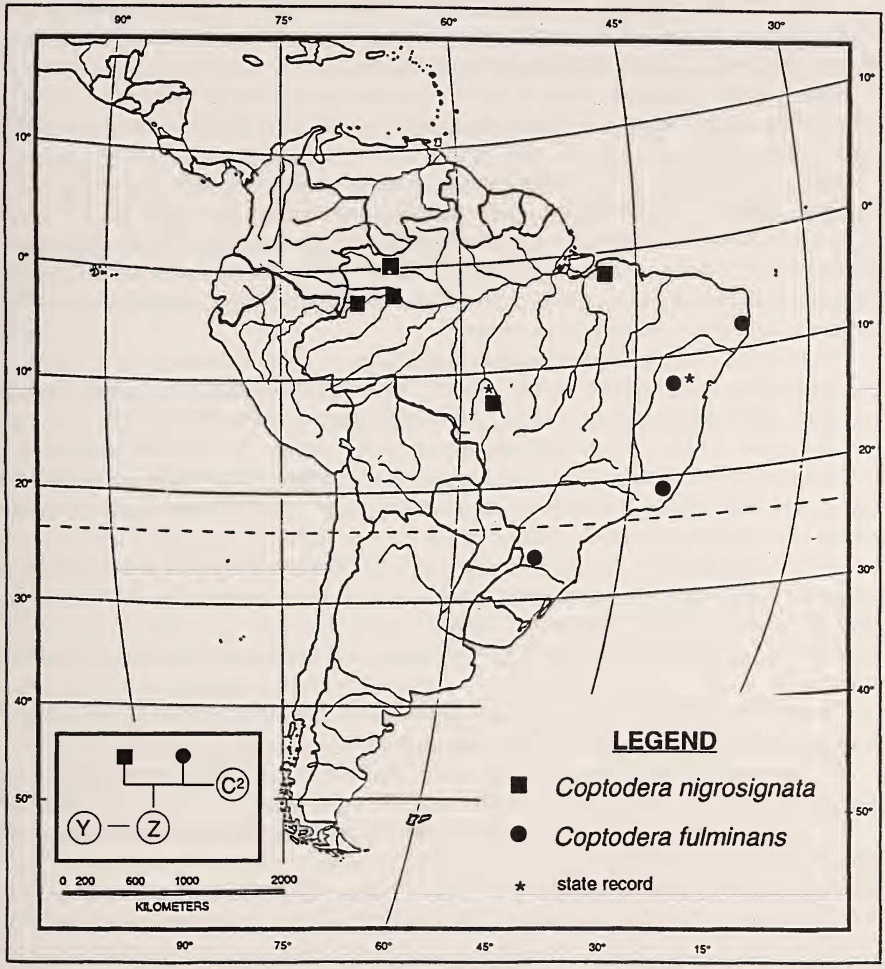
Stenoglossa nigrostriata: Chaudoir 1869: 203.

Dromius multiguttata Putzeys 1845: 377. Type material: Not located. Type locality: Cumaná, state of Sucre, Venezuela.

Stenoglossa multiguttata: Chaudoir 1869: 203.

Stenoglossa variegata Chaudoir 1848: 117. Type material: HOLOTYPE labelled: variegata type Chaud (hand written); Ex Musaeo Chaudoir (red print); HOLOTYPE Stenoglossa variegata Chd det. George E. Ball 72 [MNHP]. Type area: Venezuela.-- Chaudoir 1869: 203.

Stenoglossa pallida Bates 1869: 78. Type material: LECTOTYPE (here selected) labelled: Ega (hand written); nigrostriata Reiche pallida Bates (hand written); H.W. Bates Biol Cent Amer;



MAP 8. Geographical distribution of *Coptodera nigrosignata* (Chaudoir) and *C. fulminans* (Bates). Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

LECTO TYPE (disc); LECTOTYPE Stenoglossa pallida Bts det. George E. Ball 72 [MNHP]. Type locality: Ega, state of Amazonas, Brazil.-- Bates 1870: XVII.

Notes about synonomy.-- We were unable to locate the type of *S. multiguttata* Putzeys. K. Desender (pers. comm.) also was unable to find the type specimen in the Institut Royal des Sciences Naturelles de Belgique in Brussels. We accept Chaudoir's synonymy of *S. multiguttata*. We confirm the status of the other junior synonyms on the basis of study of type material.

Recognition.-- This species is readily separated from other species in the *C. transversa* group on a combination of three characters and geographical distribution: isodiametric elytral microsculpture, markedly developed upper spur on the inner surface of the fore tibia, elytral color pattern, and known only from northern South America.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum testaceous to brunneo-testaceous; elytra testaceous to brunneo-testaceous with rufo-brunneous to brunneous markings; appendages, antennae and mouthparts testaceous to brunneo-testaceous; ventral surface broadly testaceous to brunneo-testaceous along mid-line longitudinally, darkened to brunneous laterally, sternum 6 brunneo-testaceous to rufo-brunneous with apical margin paler; proepipleuron and elytral epipleuron testaceous to brunneo-testaceous; sternum 6 not testaceous medially.

Fixed setae. Each elytron with four discal setae.

Elytra (Fig. 20D). Apical margin sinuate; lateral margin markedly explanate in females.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

Abdominal sterna. Sterna III-V of male as in Fig. 10A.

Male genitalia. Median lobe as in Figs. 21G-21H, with apical portion in lateral-left aspect short, trianguloid, tapered gradually to apex, in dorsal aspect sides gradually tapered to apex; apex in lateral-left and dorsal aspects narrowly rounded.

Notes about habitat.-- Specimens were taken at 609 m in Colombia and at 200 m in Peru. Specimens were taken by beating during the day in a primary forest in Brazil and on logs, under bark and from a cornstone polypore in Peru.

Geographical distribution (Map 9).-- This species is known only from the Amazon Basin and northward in cis-Andean South America.

Chorological affinities.-- The range of this species is adjacent to, but is not known to overlap the range of its adelphotaxon, *C. lineata + C. stockwelli.*

Phylogenetic relationships.-- This species is the adelphotaxon of the species pair *C. lineata + C. stockwelli.*

Material examined.-- We examined 31 specimens, including types, and saw non-type material from the following localities:

BOLIVIA Cochabamba. (MNHP).

BRAZIL Amazon (MNHP); **Amazonas**. Ega (MCSN)(MNHP); 30 km w Itaquatiara, Rio Urubu (CMNH); *Mato Grosso*. (MNHP); Chapada (CMNH). Collections in November and January.

COLOMBIA Magdelena. Don Amo (CMNH). Collection in July.

COLOMBIA/PEROU (MNHP).

PERU Madre de Dios. 15 km ne Puerto Maldonado (SEMC). Collections in July.

VENEZUELA (MNHP).

Coptodera lineata (Bates), new combination

Figs. 20E, 21I, 21J, 22A & 22B; Map 9

Stenoglossa lineata Bates 1883: 184. Type material: LECTOTYPE (here selected) male, labelled: Type H.T. (disc with red border); Chacoj Vera Paz Champion; Stenoglossa lineata Bates; Stenoglossa lineata Bates (hand written); LECTOTYPE ♂ Stenoglossa lineata Bts By Erwin '76 [BMNH]. Type locality: Chacoj, state of Alta Verapaz, Guatemala.-- Ball 1975: 172.

Recognition.-- This species is readily separated from other species of the *C. transversa* group on a combination of two characters: isodiametric elytral microsculpture and elytral color pattern.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous to brunneo-testaceous; pronotum testaceous; elytra testaceous with rufo-brunneous to nearly piceous markings; appendages, antennae and mouthparts testaceous; ventral surface moderately to broadly testaceous along mid-line longitudinally, darkened to nearly piceous laterally, sternum 6 rufo-brunneous to dark brunneous with apical margin paler; proepipleuron and elytral epipleuron testaceous.

Fixed setae. Each elytron with four discal setae.

Elytra (Fig. 20E). Apical margin shallowly sinuate; lateral margin markedly explanate in females.

Legs. Well developed upper spur on inner surface of fore-tibia.

Male genitalia. Median lobe as in Figs. 21I, 21J, 22A-22B, with apical portion in lateral-left aspect very short, rectangular, in dorsal aspect trianguloid, acutely tapered; apex in lateral-left aspect broadly rounded, in dorsal aspect narrowly rounded.

Notes about habitat.-- Specimens were taken in the following countries at these altitudes: Guatemala, 731 m; México, 30-122 m; and Panamá, 243-457 m. Specimens were taken under bark, on wilted leaves and dry wood at night in Costa Rica; under bark, on logs, on dead tree in a gallery forest, on a dead log in a thorn forest, and in a rain forest in México.

Geographical distribution (Map 9).-- This range of this species extends from western Panamá northward to the Gulf and Pacific Versants of México north of the Isthmus of Tehuantepec.

Chorological affinities.-- The ranges of this species and its adelphotaxon, *C. stockwelli*, overlap in Chiriqui Province, western Panamá.

Phylogenetic relationships (Fig. 36).-- This species is the adelphotaxon of *C. stockwelli*.

Material examined.-- We examined 140 specimens, including types, and saw non-type material from the following localities:

COSTA RICA Limón. Hamburg Farm (BMNH)(USNM). Collections in February, March, May, June, August, and October.

GUATEMALA Alta Verapaz. Chacoj (BMNH); **Escuintla** Finca El Zapote, Zapote (FMNH); Pantaleon (BMNH); Zapote (BMNH)(MNHP). **Quezaltenango** Las Mercedes (BMNH); El Reposa (BMNH). Collection in July.

MÉXICO Chiapas. San Quintin (UASM); **Jalisco**. nr. Ixtapa (UASM); El Limon (UCBC); 2 km s e Las Palmas (UASM); **Quintana Roo**. 17 km nw Felipe Carrillo Puerto (RHTC); **San Luis Potosí**. Tamazunchale (CAS); **Tabasco**. La Chontalpa (USNM); **Veracruz**. Almolonga (BMNH)(USNM); Cerro de Plumas (BMNH)(MNHP); Lake Catemaco (UASM); 4 km w Sontecomapan (UASM); 25.7 km n w Tuxpan (CAS). Collections in February, April, June and December.

NICARAGUA Chontales. (BMNH).

PANAMA Chiriqui. Bugaba (BMNH)(MCZ)(USNM); 2 km n Sta. Clara, Hartmann's Finca 08°51'N 82°36'W (CNC) **Panamá**. Pozo Azul, Finca Vega near Las Nubes (CAS). Collection in April.

Coptodera stockwelli, n. sp.

Figs. 7B, 20F, 21K & 21L; Map 9

Type material.-- HOLOTYPE male, labelled: ♂ +wing; ADP 25397; PANAMA. C.Z. Madden Forest 9°06'N-79°36'W 1.2mi. E cont.div. 30 June 1974; T.L.Erwin, D.R. Whitehead Colls. running on under- side of log; Expedition #28 in notebook #3 [USNM]. ALLOTYPE female, labelled same as holotype except: ♀ +wing; ADP 25414 [USNM]. 118 PARATYPES, sex and label data as follows: 16 males same as holotype except: ADP 25398......ADP 25413 (different number on each specimen) [BMNH][CAS][CNC][MCZ][UASM][USNM]. 1 male same as holotype except: ♀ +wing; ADP 25415 [USNM]. 1 male same as holotype except: ADP 25416 [USNM]. 10 males same as holotype except: ADP 25387......ADP 25396 (different number on each specimen) [USNM]. 7 males same as holotype except: ADP 25994......ADP 2600 (different number on each specimen) [USNM]. 1 female same as allotype except: ADP 25414 [USNM]. 14 females same as allotype except: ADP 25417......ADP25430 (different number on each specimen) [BMNH][CAS][CNC][MCZ][UASM][USNM]. 1 female same as allotype except: ♂ +wing; ADP 25999 [USNM]. 2 females same as allotype except: ADP 26001 and ADP 26002 (different number on each specimen) [USNM]. 1 male and 2 females: Panamá: Canal Zone Madden Forest, Mi. 2.5 9°05'N 79°37'W 28 Jun.'72 G.Otis; running on log; ADP 47485 (male) ADP 47466 and ADP 47487 (one for each female respectively); Stenoglossa sp. (male only); [HPSC]. 3 males and 2 females: Panamá: Canal Zone Madden Forest, Mi. 2.5 9°05'N 79°37'W 13 July '74 Stockwell; running on underside of elevated log; ADP 46029, ADP 46052, ADP 46054 (one for each male respectively), ADP 460515 and ADP 46050 (one for each female respectively) [USNM]. 2 males and 3 females: PANAMA, dist. Chepo Altos de Maje 17 May 75 at lights Stockwell - Engleman; ADP 44945 and ADP 44967 (one for each male respectively), ADP 44940, ADP 44942, and ADP 44944 (one for each female respectively) [HPSC]. 1 female: PANAMA, dist. Chepo Altos de Maje 17 May 75 at lights Stockwell - Engleman [DHK]. 1 male: ♂ +winged; ADP 42864; PANAMA:Canal Zone Achiote Rd 0046 M 010.0 mi SW Gatum 0912N 07956W; under bark 01 Mar 1975 04-044 T.L.Erwin & J.L.Lawrence [USNM]. 1 male: ADP 83267; PANAMA: Canal Zone Barro Colorado Is. 10 April 1977; H. Wolda Project Light Traps Nivel SMI [USNM]. 1 male: Barro Colorado I. Canal Zone, PANAMA Jan. 17-19 1959; CNHM Panama Zool. Exped. (1959) H.S. Dybas leg.; ♂ +wing; ADP 08174 [FMNH]. 2 males and 1 female: ♀ +wing; ADP 27331 and ADP 27332 (males) and ADP 27333 (female); CANAL ZONE,Madden Forest VII-3-1974 O'Briens&Marshall [USNM]. 1 male: Paraiso CZ PanApr1411 EASchwarz; ♂ +wing; ADP 08180 [USNM]. 4 females: PANAMA:Canal Zone; Barro Colorado I. I:22:1959 leg. H.S. Dybas [FMNH]. 1 male: TrinidadRiv Pan. 1.VI.12 AugustBusck; ♂ +wing; ADP 08185 [USNM]. 2 females: Tabernilla CanalZone Panama; May 17.07; Aug. Busck Collector; ♀ +wing; ADP 08155 and ADP 08184 (one for each female respectively) [USNM]. 1 female: Alhajuelo CZ Pan; 27 May 1912; A Busck coll; ♀ +wing; ADP 08183 [USNM]. 1 female: CabimaPan May 22 11 AugustBusck; ♂ +wing; ADP 18181 [USNM]. 1 male: V. de Chiriqui 2-3000 ft. Champion; Ex Godman and Salvin; Stenoglossa nigrostriata Bates (handwritten); ♀ +wing; ADP 08154 and ADP 08156 (one for each male respectively); sten 1 (yellow paper; on first male); HOMOTYPE (red type) Stenoglossa nigrostriata R. (handwritten; on first male) [MCZ]. 4 males: V. de Chiriqui, 2-3000 ft. Champion; H.W.Bates Biol.Cent.Amer.; Museum Paris ex Coll.R. Oberthur (light green paper); Stenogl. sp. 8 Shpeley & Ball det. G.E. Ball '90 [MNHP]. 1 male and 1 female (on a single pin): Ciricito Canal Zone 2/25/30 (green paper); 11008 (green paper); 11009 (green paper); Blackwelder Collection (blue paper); ♂ +wing; ♀ +wing; ADP 08189; ADP 80190 [USNM]. 2 females (on a single pin): Ciricito Canal Zone

2/25/30 (green paper); 11010 (green paper); 11011 (green paper); Blackwelder Collection (blue paper); ♀ +wing (two labels); ADP 08187; ADP 08188 [USNM]. 1 female: CiricitoCZ Mar 20 1930 Blackwelder (blue paper); Blackwelder Collection (blue paper); ♀ +wing; ADP 08186; sten 2 (yellow paper); HOMOTYPE (red type) Stenoglossa lineata Bts (handwritten); HOMOTYPE (red type) Stenoglossa nigrosignata Chd. (handwritten); HOMOTYPE (red type); Stenoglossa variegata Chd. (handwritten) [USNM]. 1 male: PANAMA: Bayano Dist. 2 km. W Ipeti 22 May 1991 R. Turnbow [RHTC]. 1 male: PANAMA: Panama Prov. 11-15 km. N El Llano 24 May 1991 R. Turnbow [RHTC].

Type locality.-- Madden Forest, Canal Zone, Panamá.

Derivation of specific epithet.-- Latinized surname of Dr. Henry P. Stockwell, renowned coleopterist of the Panamá Canal Zone, who collected several of the type specimens.

Recognition.-- This species is readily separated from other species of the *C. transversa* group on a combination of three characters and geographical distribution: isodiametric elytral microsculpture, markedly developed upper spur on the inner surface of the fore-tibia, elytral color pattern and known only from Panamá.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous to nearly rufo-testaceous; pronotum testaceous; elytra testaceous with rufo-brunneous to nearly piceous markings; appendages, antennae and mouthparts testaceous; ventral surface broadly testaceous along mid-line longitudinally, darkened to brunneous laterally, sternum 6 brunneo-testaceous to rufo-testaceous with apical margin paler; proepipleuron and elytral epipleuron testaceous.

Fixed setae. Each elytron with four discal setae.

Pronotum. As in Fig. 7B.

Elytra (Fig. 20F). Apical margin sinuate; lateral margin markedly explanate in females.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

Male genitalia. Median lobe as in Figs. 21K-21L, with apical portion in lateral-left aspect very short, rectangular, in dorsal aspect with sides nearly parallel; apex in lateral-left aspect broadly rounded, in dorsal aspect narrowly rounded.

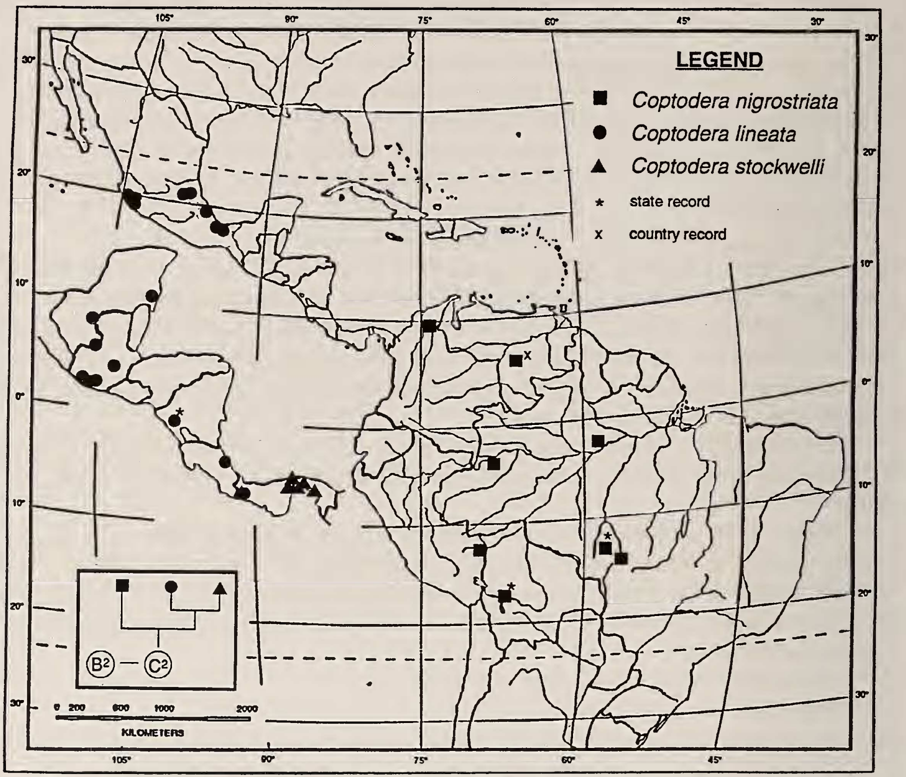
Notes about variation.-- Six specimens (1 MCZ, 4 MNHP, and 1 USNM) collected at Volcan Chiriqui have a bicolored pronotum, but the male genitalia are identical to those of other specimens of this species. The central area of the elytral disc is pale, with a longitudinal rufo-brunneous marking on each side before the pale lateral margin.

Notes about habitat.-- Specimens were taken at 46-914 m in Panamá at light, on logs, on cut wood at night, and under bark.

Geographical distribution (Map 9).-- This species is known only from Panamá, in Lower Central America.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for *C. lineata* above, the adelphotaxon of *C. stockwelli.*

Material examined.-- Type material only, see above for details.



MAP 9. Geographical distribution of *Coptodera nigrostriata* (Reiche), *C. lineata* (Bates) and *C. stockwelli*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Coptodera transversa (Reiche), new combination

Figs. 3A-3F, 10B, 12E-12H, 20G, 21M & 21N; Map 10

Tetragonoderus transversus Reiche 1843: 179. Type material: LECTOTYPE (here selected) male, labelled: Tetragonoderus (hand written); transversus Reiche Rev. Cuvier 1843; Ex Musaeo Chaudoir (red print) [MNHP]. Type area: Colombia.

Stenoglossa transversa: Chaudoir 1869:204.

Stenoglossa atriceps Bates 1869: 78. Type material: LECTOTYPE (here selected) male, labelled: Ega (hand written); transversa Reiche atriceps Bates (hand written); H.W. Bates Biol. Cent. Amer.; LECTO TYPE (disc); LECTOTYPE Stenoglossa atriceps Bts det. George E. Ball 72 [MNHP]. Type locality: Ega, state of Amazonas, Brazil.-- Bates 1870: XVII.

Stenoglossa picturata Chaudoir 1869: 205. NEW SYNONOMY. Type material: LECTOTYPE (here selected) male, labelled: picturata Chaudoir Amerique Sallé; Ex Musaeo Chaudoir (red print); LECTO TYPE (disc); LECTOTYPE Stenoglossa picturata Chd det. George E. Ball 72 [MNHP]. Type area: México.

Stenoglossa undulata Chaudoir 1869: 206. NEW SYNONOMY. Type material: LECTOTYPE (here selected) female, labelled: undulata Chaud Brésil Nov Frib. Squires (hand written); Squires; Ex Musaeo Chaudoir (red print); LECTO TYPE (disc); LECTOTYPE Stenoglossa undulata Chd det. George E. Ball 72 [MNHP]. Type locality: Nova Friburgo, state of Rio de Janeiro, Brazil.

Notes about synonomy.-- The type specimens associated with the junior synonyms recorded above do not differ significantly from the type specimen of *C. transversa* Reiche.

Recognition.-- This species is readily separated from other species in the *C. transversa* group on a combination of two characters: transverse elytral microsculpture and markedly reduced upper spur on the inner surface of the fore-tibia.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head brunneous to piceous; pronotum bicolored, disc dark testaceous to nearly piceous, anterior and lateral margins testaceous to nearly piceous, posterior margin testaceous; elytra testaceous with brunneo-testaceous to piceous markings; appendages and antennae dark testaceous to nearly brunneous; mouthparts brunneo-testaceous to dark brunneous; femora dark brunneous in basal two third; ventral surface rufo-testaceous to nearly piceous, sternum 6 with apical margin paler; elytral epipleuron testaceous.

Fixed setae. Each elytron with three discal setae.

Mouthparts. Mandibles as in Figs. 3A-3F.

Elytra (Fig. 20G). Apical margin sinuate; lateral margin markedly explanate in females.

Legs. Markedly reduced upper spur on the inner surface of the fore-tibia.

Abdominal sterna. Sterna III-V of male as in Fig. 10B.

Male genitalia. Median lobe as in Figs. 21M-21N, with apical portion in lateral-left aspect very short, quadrate, hardly tapered to apex, in dorsal aspect with sides slightly tapered; apex in lateral-left aspect broadly rounded, in dorsal aspect narrowly rounded.

Ovipositor. Stylomere 2 as in Figs. 12E-12H.

Notes about habitat.-- Specimens were taken in the following countries at these altitudes: Brazil, 100-500 m; Costa Rica, 1380-1390 m; Guatemala, 1400-2100 m; México, 30 to 2164 m; and Panamá, 1219-1524 m. Specimens were taken on tree trunks in Costa Rica; under bark and at u-v light in Guatemala; in a cloud forest, under bark, on logs and on bark of a recently fallen tree in México and in a light trap in Panamá.

Geographical distribution (Map 10).-- The range of this species extends from the Southern Atlantic zone of Eastern Brazil to cis-Andean Bolivia and Paraguay, and northward through the Amazon Basin and Lower and Nuclear Central America to the Pacific and Gulf Versants of México north of the Isthmus of Tehuantepec.

Chorological affinities.-- The range of this species overlaps the range of its adelphotaxon, *C. sigillata* + *C. squiresi.*

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of the species pair *C. sigillata* + *C. squiresi.*

Material examined.-- We examined 280 specimens, including types, and saw non-type material from the following localities:

BOLIVIA Cochabamba. (MNHP).
BRAZIL Amazons (MNHP); **Amazonas.** Ega (MNHP); 30 km w Itaquatiara, Rio Urubu (CMNH); Manaus, 1 km w w Taruma Falls (CMNH); **Goias.** Jatahy (MNHP); Rio verde (MNHP); **Rio de Janeiro** Nov. Frib. (MNHP); Rio Jan. (MNHP); **Santa Catarina.** Nova Teutonia (BMNH)(CAS)(UASM)(USNM); **São Paulo.** (BMNH). Collections in all months of the year except February.
COLOMBIA.(MNHP).
COSTA RICA Limón. Hamburg Farm (USNM); **Puntarenas.** Monteverde (USNM); Monteverde, road to electric plant (USNM). Collections in June and August.
GUATEMALA Sacatepéquez. Finca San Rafael (FMNH); **Zacapa.** Sierra del Espiritu Santo, 3 km se La Union (UASM). Collections made in June.
MÉXICO Chiapas. 9.8 km n Ocosingo (RHTC); **Oaxaca.** Oaxaca (BMNH); **Queretero.** 8.3 km w San Luis Potosí Queretero border, Hwy. 120 (SEMC); **San Luis Potosí.** 29 km sw Tamazunchale (UCBC); **Veracruz.** Almolonga (BMNH)(MNHP); Cerro de Plumas (MNHP); 7 km n Huatusco (UASM); Jacale (BMNH); Jalapa (BMNH)(MNHP); 4 km w Sontecomapan (UASM). Collections in April and June to August.
PANAMA Canal Zone. Barro Colorado (USNM); **Chiriqui.** Boquete 08°48'N 82°26'W (USNM); Boquete 08°47'N 82°26'W (USNM); Bugaba (BMNH)(MNHP); Fortuna 08°44'N 82°15'N (USNM); Hartmann's Finca, 2 km n Sta. Clara 08°51'N 82°36'W (CNC); (USNM); Ojo de Agua, 4 km n Sta. Clara (USNM); V. de Chiriqui (BMNH)(MNHP); **Panamá.** Cerro Campana, Nr. Chica (USNM). Collections in April to June.
PARAGUAY Alto Paraná. Puerto P. Stroessner (HNHM). Collection in January.

Coptodera sigillata, n. sp.
Figs. 20H, 21O & 21P; Map 10

Type material.-- HOLOTYPE male, labelled: BRAZIL,Santa Cata- rina,Nova Teutonia II - 1977 Fritz Plaumann Cal.Acad.Sci.Coll. [CAS].

Type locality.-- Nova Teutonia, state of Santa Catarina, Brazil.

Derivation of specific epithet.-- From Latin *signum*, in allusion to the markedly defined dark markings on the elytra.

Recognition.-- This species is readily separated from the other species of the *C. transversa* group on a combination of three characters: transverse elytral microsculpture, markedly developed upper spur on the inner surface of the fore-tibia, and rounded sutural angle of the elytron.

Description.-- Character states of the *C. transversa* group and the following. See Tables II, IV and VI for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head rufo-brunneous; pronotum bicolored, disc rufo-brunneous, broad testaceous lateral margins, narrower testaceous anterior and posterior margins; elytra testaceous with dark brunneous to piceous markings; appendages, antennae and mouthparts testaceous to slightly darker; ventral surface broadly testaceous along mid-line longitudinally, darkened to dark brunneous laterally, sternum 6 rufo-brunneous with apical margin paler; proepipleuron and elytral epipleuron testaceous.

Fixed setae. Each elytron with three discal setae.

Elytra (Fig. 20H). Apical margin sinuate.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

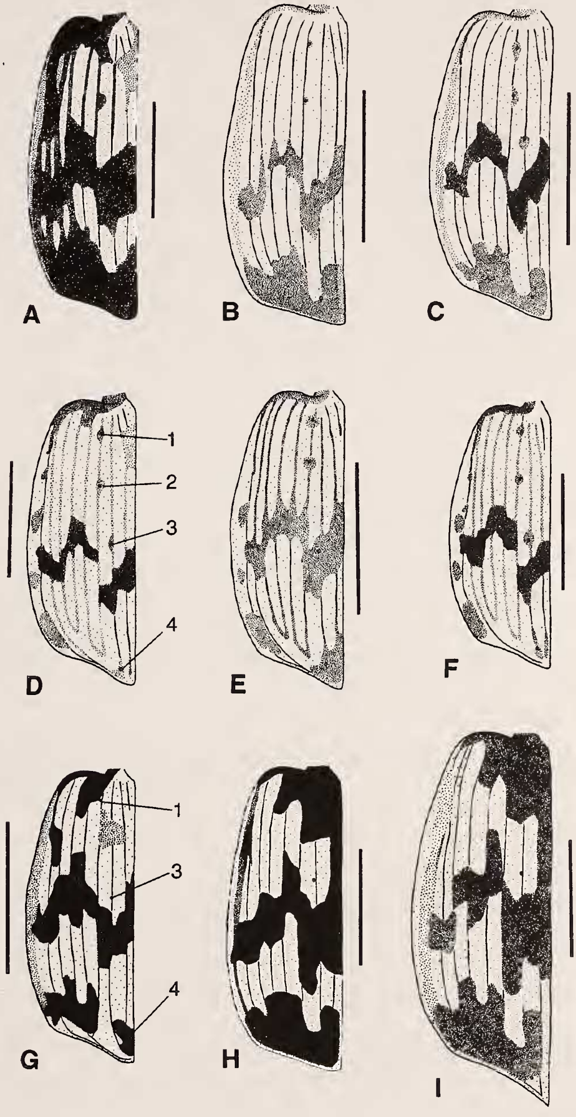


FIGURE 20. Line drawings of left elytron of *Coptodera transversa* group, dorsal aspect. Fig. A: *C. dromioides* (Bates). Fig. B: *C. nigrosignata* (Chaudoir). Fig. C: *C. fulminans* (Bates). Fig. D: *C. nigrostriata* (Reiche). Fig. E: *C. lineata* (Bates). Fig. F: *C. stockwelli*, new species. Fig. G: *C. transversa* (Reiche). Fig. H: *C. sigillata*, new species. Fig. I: *C. squiresi* (Chaudoir). Scale bars = 1 mm. Legend: 1, discal setigerous puncture #1; 2, discal setigerous puncture #2; 3, discal setigerous puncture #3; 4, discal setigerous puncture #4.

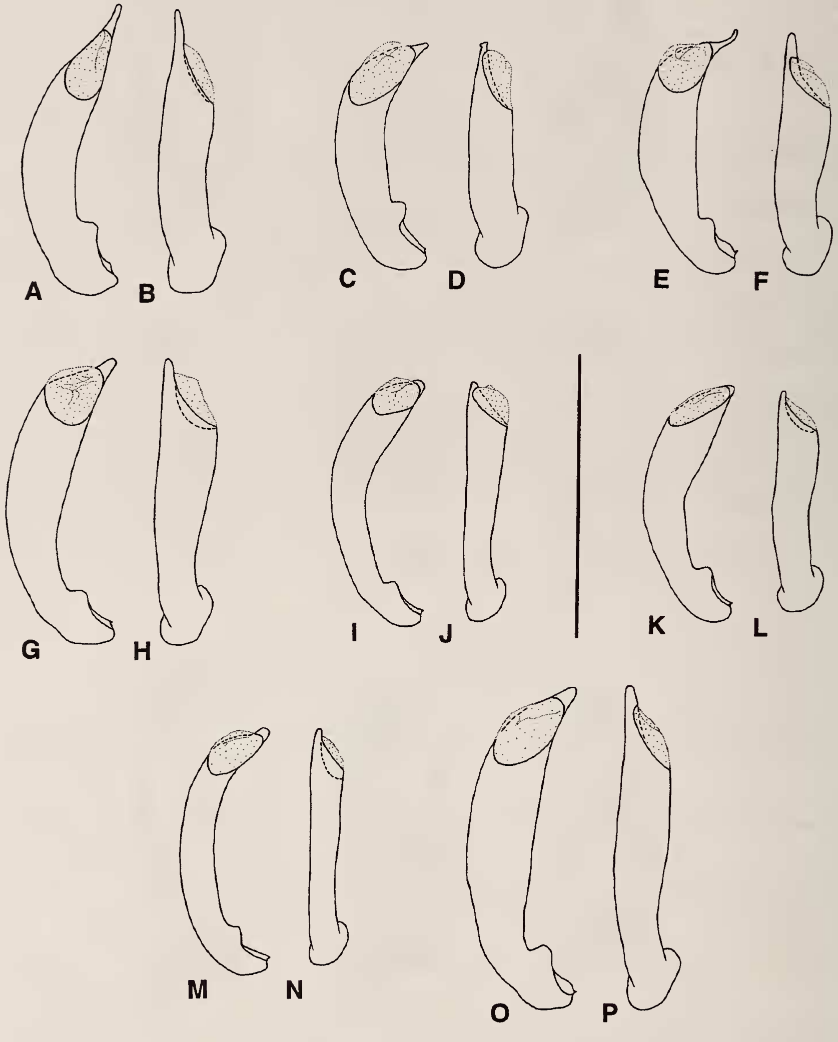


FIGURE 21. Line drawings of male genitalia of *Coptodera transversa* group. Figs. A, C, E, G, I, K, M & O left lateral aspect. Figs. B, D, F, H, J, L, N & P dorsal aspect. Figs. A-B: *C. dromioides* (Bates). Figs. C-D: *C. nigrosignata* (Chaudoir). Figs. E-F: *C. fulminans* (Bates). Figs. G-H: *C. nigrostriata* (Reiche). Figs. I-J: *C. lineata* (Bates). Figs. K-L: *C. stockwelli*, new species. Figs. M-N: *C. transversa* (Reiche). Figs. O-P: *C. sigillata*, new species. Scale bars = 1 mm.

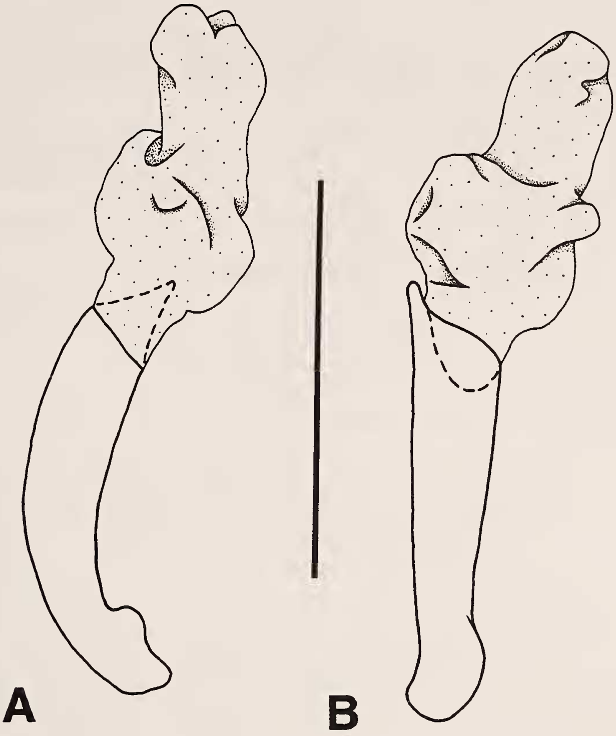


FIGURE 22. Line drawings of male genitalia of *C. lineata* (Bates). Figs. A & B left lateral and dorsal aspects respectively. Scale bars = 1 mm.

Male genitalia. Median lobe as in Figs. 21O-21P, with apical portion in lateral-left aspect very short, trianguloid, tapered gradually to apex, in dorsal aspect nearly parallel, hardly tapered; apex in lateral-left and dorsal aspects narrowly rounded.

Notes about habitat.-- None available.

Geographical distribution (Map 10).-- This species is known only from the type locality of Nova Teutonia, Santa Catarina, Brazil.

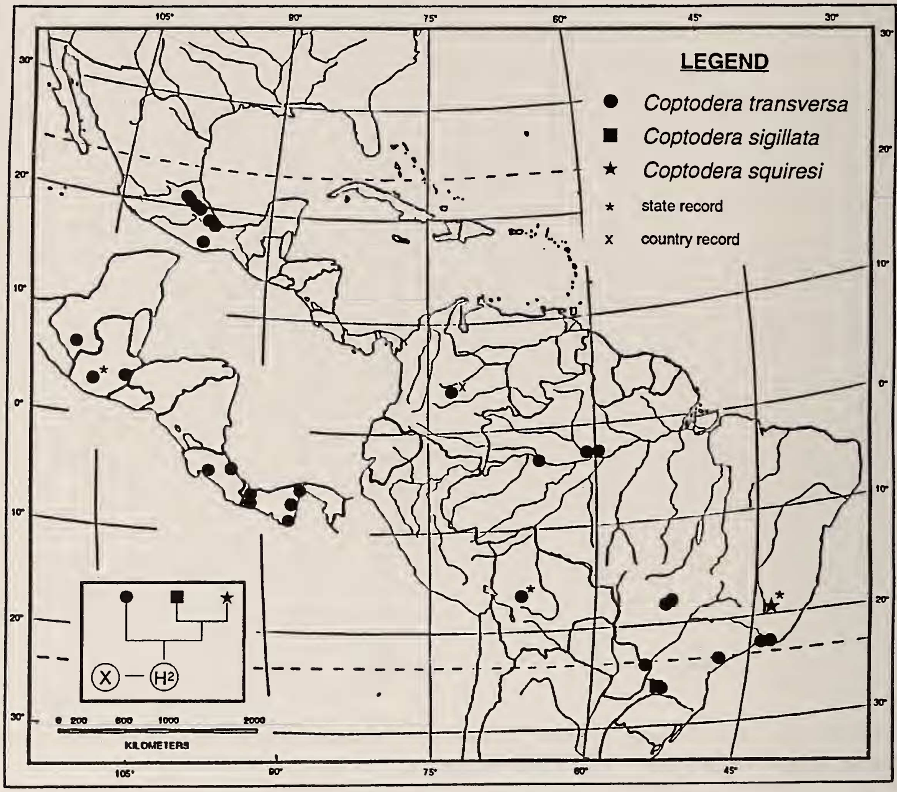
Chorological affinities.-- Both *C. sigillata* and its adelphotaxon are known from the Southern Atlantic zone of Eastern Brazil, but from different localities therein.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. squiresi.*

Material examined.-- Holotype only, see above for details.

Coptodera squiresi (Chaudoir), new combination
Fig. 20I; Map 10

Stenoglossa squiresi Chaudoir 1869: 201. Type Material: LECTOTYPE female, labelled: Ex Musaeo Chaudoir (red ink); HOLO (red paper); TYPE (red paper); Squiresii Chaud. Brésil



MAP 10. Geographical distribution of *Coptodera transversa* (Reiche), *C. sigillata*, new species and *C. squiresi* (Chaudoir). Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Minas Squires (hand written); MUSEUM PARIS 1962 COLL. R. OBERTHUR; HOLOTYPE Stenoglossa squiresi Chd det. George E. Ball 72 [MNHP]. Type area: State of Minas Gerais, Brazil.

Recognition.-- This species is readily separated from the other species of the *C. transversa* group by the acute sutural angle of the elytron.

Description.-- Character states of the *C. transversa* group and the following. See Tables III, V, and VII for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head rufo-brunneous; pronotum bicolored, disc rufo-brunneous, broad testaceous lateral margins, narrower testaceous anterior and posterior margins; elytra testaceous with rufo-brunneous markings; appendages, antennae and mouthparts testaceous; tibiae slightly darkened medially; ventral surface of pronotum, sterna medially and elytral epipleuron testaceous, remainder of ventral surface dark testaceous to brunneous; sternum 6 not testaceous medially.

Fixed setae. Each elytron with three discal setae.

Elytra (Fig. 20I). Sutural angle acute; apical margin sinuate; lateral margin moderately explanate in female.

Legs. Well developed upper spur on inner surface of fore-tibia.

Male genitalia. Male unknown.

Notes about habitat.-- None available.

Geographical distribution (Map 10).-- This species is only known from the type area of Minas Gerais in Brazil.

Chorological affinities and phylogenetic relationships.-- See these topics for *C. sigillata* above, the postulated adelphotaxon of *C. squiresi.*

Material examined.-- Holotype only, see above for details.

Coptodera festiva Group

This group has nine species which are characterized by a shallowly emarginate anterior margin of the labrum that is wider than long, four discal setigerous punctures on each elytron, elytra with a variegated color pattern, markedly developed upper spur on the inner surface of the fore-tibia, and mid-tibia of male with notch on the ventral surface near apex. See Table I for features of mandibles. Male genitalia with median lobe pleuropic-left; membranous portion various degrees of "medium"; internal sac with macrospines (Figs. 24A-24P). Ovipositor with ensiform setae of stylomere 2 on dorsal margin (cf. Fig. 12I); nematiform setae present. The geographical range of this group extends from the Southern Atlantic zone of Brazil northward through the Amazon Basin of cis-Andean South America, Lower and Nuclear Central America to México north of the Isthmus of Tehuantepec, the Greater Antilles and Southern Florida.

Chorological affinities.-- The geographical range of the *C. festiva* group is broadly overlapped by the combined ranges of its adelphotaxa, the *C. bifasciata*, *C. emarginata*, *C. picea* and *C. aerata* groups (Maps 11-20).

Phylogenetic relationships (Fig. 35).-- The *C. festiva* group is the adelphotaxon of the *C. bifasciata* - *C. aerata* group lineage.

Coptodera sahlbergi Chaudoir
Figs. 7C, 23A, 24A & 24B; Map 11

Coptodera sahlbergi Chaudoir 1869: 181. Type material: HOLOTYPE female, labelled: Ex Musaeo Chaudoir (red print); TYPE (red paper); Sahlbergi Chaud. Brésil Petropolis Sahlb. jun. (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Petropolis, Rio de Janeiro, Brazil.

Coptodera discicollis Chaudoir 1869: 181. NEW SYNONYMY. Type material: HOLOTYPE female, labelled: Bolivie (handwritten on light green paper); Ex Musaeo Chaudoir (red print); Discicollis Chaud. Bolivie Deyrolle (original box label); Museum Paris ex Coll R. Oberthür light green paper) [MNHP]. Type area: Bolivia.

Notes about synonymy.-- Chaudoir's two species names were based on two specimens which we believe to be conspecific. The specimen of *C. sahlbergi* shows reduced pale markings on the elytra, while *C. discicollis* has extensive pale markings. In all other regards, the two specimens are identical.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head rufo-brunneous to dark brunneous; pronotum rufo-brunneous to rufo-piceous with broad testaceous lateral margins; elytra brunneous to rufo-piceous, with testaceous markings; lateral margin of elytra testaceous; appendages, antennae, and mouthparts testaceous to brunneo-testaceous, tibiae and apices of femora darkened. Dorsal surface with greenish to aeneous lustre. Ventral surface testaceous except proepisternum, mesepisternum, mesepimeron, metasternum (laterally), metepisternum, and epipleuron at shoulder brunneo-testaceous to brunneous.

Pronotum. As in Fig. 7C.

Elytra (Fig. 23A). Interneurs finely punctulate.

Male genitalia. As in Figs. 24A-24B, median lobe with membranous portion medium-long; apical portion medium-short, in lateral aspect triangular, tapered gradually toward apex, in dorsal aspect rod-like, sides parallel; apex in lateral aspect narrowly rounded, in dorsal aspect subtruncate. Internal sac spine A long; spine group B absent; spine group C with two long spines.

Notes about habitat.-- Specimens were taken in Brazil at altitudes of 300-700 m; in Paraguay at night.

Geographical distribution (Map 11).-- The known range of this species in South America extends from the southern edge of the Amazon Basin southward to northern Argentina and eastward to the Southern Atlantic zone.

Chorological affinities.-- The range of this species is allopatric to the ranges of most species in the *C. festiva* group, being overlapped by the most distantly related species pair, only (*C. rufescens* + *teutonica*, Map 12).

Phylogenetic relationships (Fig. 36).-- This species is the adelphotaxon of the remaining species in the *C. festiva* group.

Material examined.-- We examined 54 specimens, including types, and saw non-type material from the following localities:

ARGENTINA Tucumán. Tucumán (BMNH). Collection was made in October.

BRAZIL (HNHM); Amazon (MCZ); **Espirito Santo**. Espirito Santo (UASM); **Mato Grosso**. Chapada (=Chapada dos Guimaraes (CMNH); R. Caraguata (MCZ); **Minas Gerais**. Aguas Vermelhas (CMNH); **Parana**. Rolandia (AMNH)(MCZ); **Rio de Janeiro**. Itatiaya (BMNH); Lagune de Sacuaresma (MNHP); Rio de Jan. (CMNH); **Santa Catarina**. Nova Teutonia (CAS)(IZWP)(MCZ)(ZSMM); **São Paulo**. Barueri (MCZ)(MZSP); Campos Fordao (USNM); Faz. Itaquerê, Nova Europa (MZSP); Faz. Pau d'Alho Itú (MZSP); S. Paulo (HNHM); Val. du Rio Pardo (MNHP). Collections were made in September to April.

PARAGUAY Amambay. (MCZ); **Parahuarí**. Parc. Nac. Ybycuí (JKOC). Collection was made in January.

One specimen from the MCZ labelled "Santiago". One specimen from MNHP with a handwritten label that appears to be "Cuba", and if our interpretation is correct, then the specimen must be mislabelled.

Coptodera relucens Bates

Figs. 23B, 23C, 24C & 24D; Map 11

Coptodera relucens Bates 1869: 73. Type material: LECTOTYPE (here selected) male, labelled: LECTO (red paper); TYPE (red paper); (green rectangle); Ex Musaeo Chaudoir (red print); relucens Bates Amazone Ega Bates (original box label); Coptodera relucens Bates det. G.E.

Ball '87; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega, Amazonas, Brazil.

Coptodera lebioides Bates 1869: 74. NEW SYNONYMY. Type material: LECTOTYPE (here selected) male, labelled: Ega (handwritten); TYPE (red paper); Ex Musaeo H.W. Bates 1892; Lebioides Bates (handwritten); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega, Amazonas, Brazil.

Coptodera rotundipennis Chaudoir 1869: 182. Type material: LECTOTYPE (here selected) male, labelled: rotundipennis Chaud (handwritten); Ex Musaeo Chaudoir (red print); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega, Amazonas, Brazil.-- Bates 1870: XVI.

Note about synonymy.-- After examining the types of *C. relucens* and *C. lebioides*, we believe the two to be conspecific.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head rufo-testaceous to rufous, darkened medially or not; pronotum brunneo-testaceous to rufous, with aeneous lustre, with one longitudinal rufo-piceous marking each side of median line, lateral margin diffusely paler or not; elytra rufous to rufo-piceous, with aeneous lustre, and testaceous or dirty white markings; lateral margin of elytra testaceous; appendages, antennae, and mouthparts testaceous, tibiae and tarsomeres darkened. Ventral surface testaceous to rufo-testaceous.

Elytra (Figs. 23B-23C). Interneurs punctate.

Male genitalia. As in Figs. 24C-24D, median lobe with membranous portion medium-long; apical portion medium-long, in lateral aspect slender, spiculate, tapered apically, in dorsal aspect slender, sides parallel; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A medium in length; spine group B with two long spines; spine group C with one long spine.

Notes about variation.-- This species exhibits two elytral color patterns, but the male genitalia are identical, indicating that both forms must be conspecific.

Notes about habitat.-- None available.

Geographical distribution (Map 11).-- This species is known only from the Amazon Basin, in Brazil.

Chorological affinities.-- This species and its adelphotaxon, *C. poecila*, are allopatric.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. poecila.*

Material examined.-- We examined 8 specimens, including types, and saw non-type material from the following localities:

BRAZIL Amazonas. Ega (BMNH)(MNHP); **Mato Grosso**. Chapada (=Chapada dos Guimares (CMNH); **Para**. Santarem (CMNH). Not located "Chimboanga" (MNHP).

Coptodera poecila Bates
Figs. 23D, 24E & 24F; Map 11

Coptodera poecila Bates 1883: 183. Type material: HOLOTYPE male, labelled: Type HT (disc bordered with red); V. de Chiriqui 25-4000 ft. Champion; B.C.A. Col. I.1 Coptodera poecila, Bates; Coptodera poecila Bates (Bates' handwriting); HOLOTYPE ♂ Coptodera poecila Bates by Erwin '76 [BMNH]. Type locality: Volcan de Chiriqui, Chiriqui Prov., Panamá.

Description.-- Character states of the *C. festiva* group and the following. See Tables II, IV and VI for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum testaceous; elytra rufo-piceous with testaceous markings; antennae testaceous, antennomeres 2-4 darkened; mouthparts rufo-testaceous to rufo-brunneous (apical half of terminal palpomeres testaceous); femora testaceous, darkened apically; tibiae and tarsi dark brunneous. Dorsally, dark areas of elytra with faint green lustre. Ventral surface testaceous; metepisternum and metasternum rufo-testaceous; epipleuron rufo-piceous.

Elytra (Fig. 23D). Interneurs finely punctate.

Male genitalia. As in Figs. 24E-24F, median lobe with membranous portion medium-short; apical portion medium-long, in lateral aspect slender, tapered apically, in dorsal aspect slender, sides parallel; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A medium in length; spine group B with two long spines; spine group C with two medium-short spines.

Notes about habitat.-- None available.

Geographical distribution (Map 11).-- This species is known only from the type locality, in Lower Middle America.

Chorological affinities.-- The type locality of this species is overlapped by the range of *C. festiva*, but it is separated from the range of its adelphotaxon, *C. relucens*.

Phylogenetic relationships (Fig. 36).-- See this topic for *C. relucens* above, the adelphotaxon of *C. poecila*.

Material examined.-- Holotype only.

Coptodera pakitza, new species

Fig. 23E; Map 11

Type material.-- HOLOTYPE, female labelled: PERU: MADRE DE DIOS Pakitza T.L.Erwin 29-Oct - 01Nov90 12°07'S 70°58'W; Forest type #12, on trunks along trail at Tr. Tachigali /42; BIOLAT/COLE 000008389 [USNM]. One female PARATYPE labelled same as holotype except third label is as follows: BIOLAT/COLE 000008385 [USNM].

Type locality.-- Pakitza, department of Madre de Dios, Peru.

Derivation of specific epithet.-- From "Pakitza", the name of the type locality.

Description.-- Character states of the *C. festiva* group and the following. See Tables III, V and VII for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head dark testaceous; pronotum bicolored, rufo-piceous macula surrounded with markedly broad testaceous lateral margins, anterior and posterior margins testaceous also; elytra dark brunneous to rufo-piceous with testaceous markings; lateral margin of elytron testaceous; appendages, antennae and mouthparts testaceous. Dark markings of dorsal surface with moderate green lustre, pale areas of elytra with faint green lustre. Ventral surface testaceous, abdominal sterna darkened laterally, thoracic sterna brunneo-testaceous to dark brunneous (elytral epipleuron testaceous).

Elytra (Fig. 23E). Interneurs finely punctate.

Male genitalia. Unknown.

Notes about habitat.-- Both specimens were taken on tree trunks along a forest trail.

Geographical distribution (Map 11).-- This species is known only from the type locality in southern cis-Andean Peru, in the upper reaches of the Amazon Basin.

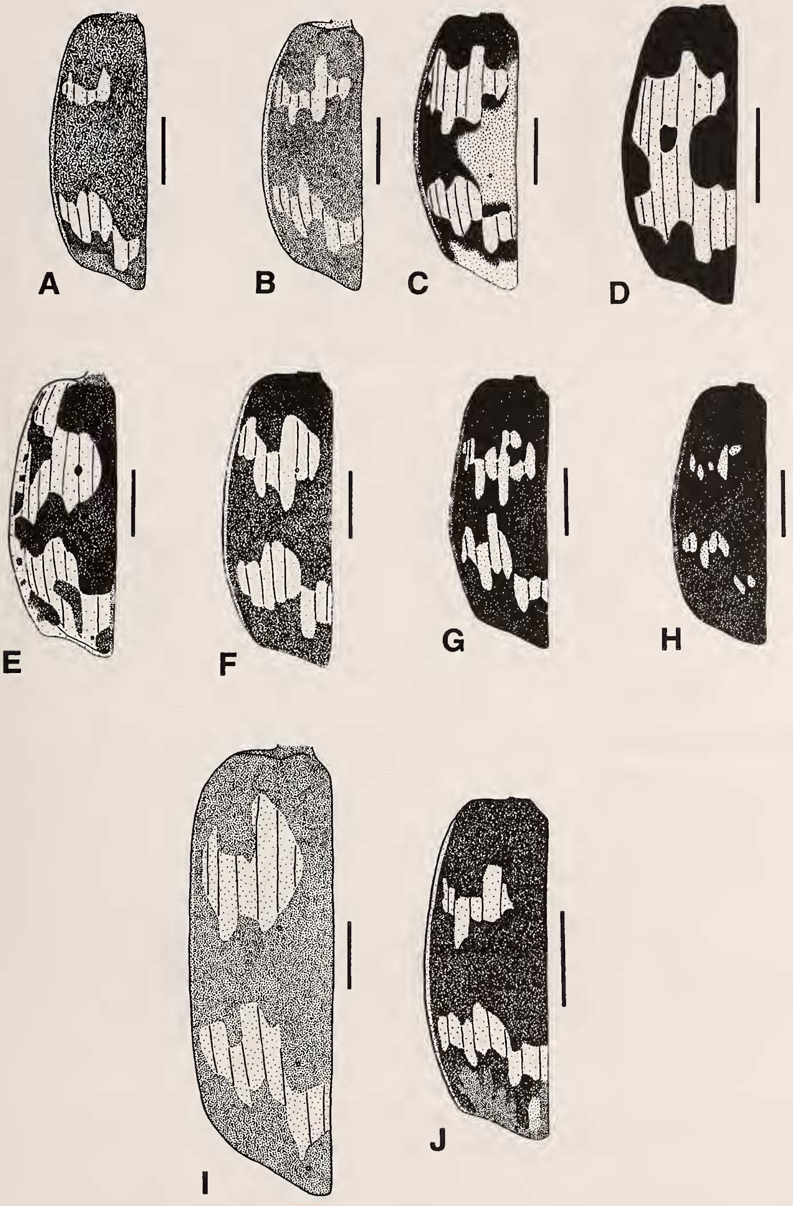


FIGURE 23. Line drawings of left elytron of *Coptodera festiva* group, dorsal aspect. Fig. A: *C. sahlbergi* Chaudoir. Figs. B-C: *C. relucens* Bates. Fig. D: *C. poecila* Bates. Fig. E: *C. pakitza* new species. Fig. F: *C. festiva* Dejean. Fig. G. *C. foveolata*, new species. Fig. H: *C. nigroviridis*, new species. Fig. I: *C. rufescens* Buquet. Fig. J: *C. teutonica*, new species. Scale bars = 1 mm.

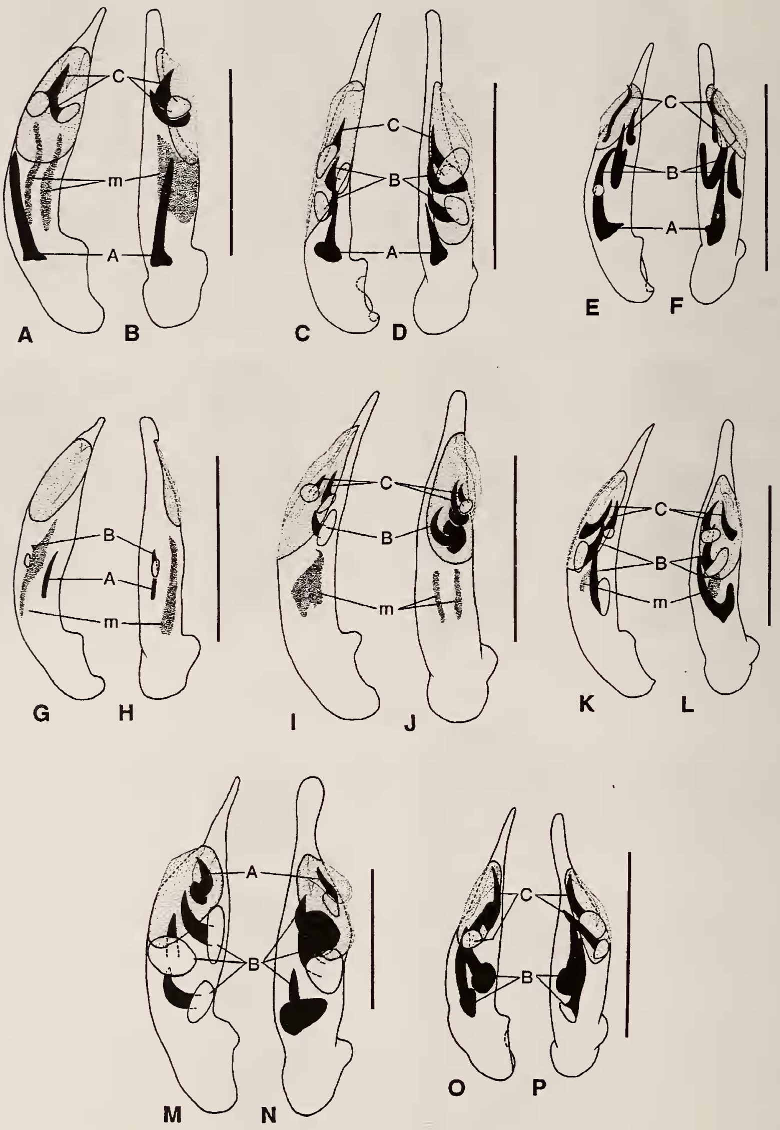
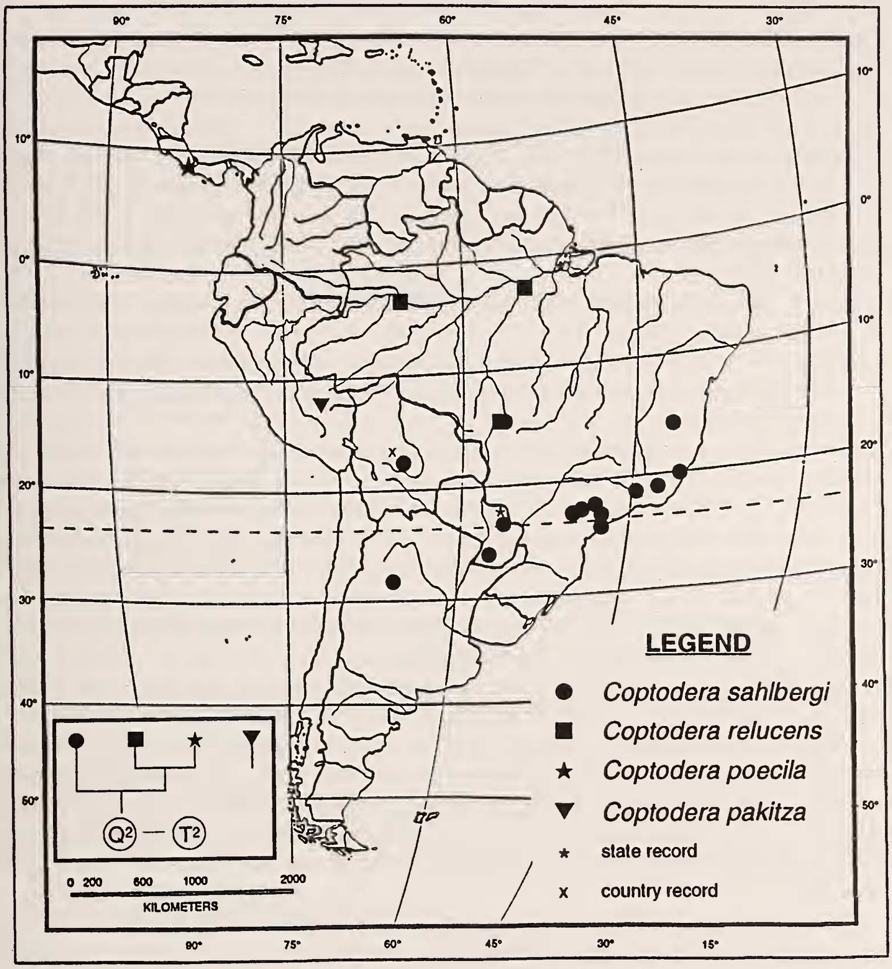


FIGURE 24. Line drawings of male genitalia of *Coptodera festiva* group. Figs. A, C, E, G, I, K, M & O left lateral aspect. Figs. B, D, F, H, J, L, N & P dorsal aspect. Figs. A-B: *C. sahlbergi* Chaudoir. Figs. C-D: *C. relucens* Bates. Figs. E-F: *C. poecila* Bates. Figs. G-H: *C. festiva* Dejean. Figs. I-J. *C. foveolata*, new species. Figs. K-L: *C. nigroviridis*, new species. Figs. M-N: *C. rufescens* Buquet. Figs. O-P: *C. teutonica*, new species. Scale bars = 1 mm. Legend: A, spine A; B, spine B; C, spine C; m, microtrichial field.



MAP 11. Geographical distribution of *Coptodera sahlbergi* Chaudoir, *C. relucens* Bates, *C. poecila* Bates and *C. pakitza*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Chorological affinities.-- The ranges of the other species in the *C. festiva* group do not overlap that of *C. pakitza*.

Phylogenetic relationships (Fig. 36).-- The position of this species is unresolved due to the lack of a male specimen; it is placed tentatively next to the *C. relucens* - *C. poecila* and *C. festiva* - *C. teutonica* lineages.

Material examined.-- Type material only, see above for details.

Coptodera festiva Dejean
Figs. 1E, 3G-3L, 23F, 24G & 24H; Map 12

Coptodera festiva Dejean 1825: 274. Type material: LECTOTYPE male, labelled: festiva mihi in ins. Cuba (Dejean handwriting on green paper); D. Ericher (Dejean handwriting on green paper); Ex Musaeo Chaudoir (red print); TYPE (red paper); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Cuba.-- Chaudoir 1869: 182.-- Erwin & Sims 1984: 446.

Coptodera chloris Bates 1883: 182. NEW SYNONYMY. Type material: LECTOTYPE (here selected) male, labelled: Type H.T. (disc with red border); Mirador Mexico Hoege; B.C.A. Col. I.1 Coptodera chloris, Bates; Coptodera chloris Bates (handwritten [Bates']); LECTOTYPE ♂ Coptodera chloris Bates by Erwin '76 [BMNH]. Type locality: Mirador, Veracruz, México.

Notes about type material.-- In the BMNH are two additional male specimens, labelled: Mirador Mexico Hoege; B.C.A. Col. I.1 *Coptodera chloris*, Bates; and are here selected as PARALECTOTYPES. In the MNHP are two female specimens labelled: Mirador Mexico Hoege; H.W. Bates Biol Cent Amer; Museum Paris ex Coll R. Oberthür (light green paper); and are here selected as PARALECTOTYPES (one of the two specimens also bears a "TYPE" label on red paper).

Notes about synonymy.-- The type specimens of *C. festiva* and *Coptodera chloris* Bates are identical, and we believe them to be conspecific.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous to darkened medially; pronotum testaceous to brunneo-testaceous with disc slightly to broadly darkened each side of the mid-line; elytra brunneous to rufo-piceous, faint greenish to aeneous lustre (best observed basally), with testaceous markings; lateral margin of elytra testaceous; appendages, antennae, and mouthparts testaceous to rufo-testaceous. Ventral surface testaceous with epipleuron at shoulder brunneo-testaceous to brunneous (see notes on variation).

Mouthparts. Labrum as in Fig. 1E; mandibles as in Figs. 3G-3L.

Elytra (Fig. 23F). Interneurs impunctate.

Male genitalia. As in Figs. 24G-24H, median lobe with membranous portion medium-short; apical portion short, in lateral aspect trianguloid, tapered irregularly, rather bulbous, in dorsal aspect broader, sides about parallel; apex in lateral aspect narrowly rounded, in dorsal aspect more broadly rounded. Internal sac spine A short; spine group B with one short spine; spine group C absent.

Notes about habitat.-- In Costa Rica, specimens were taken at altitudes of 200-300 m. In Cuba, specimens were taken at altitudes of 182-914 m; in a wood pile. In Haiti specimens were taken at an altitude of 305 m. In México specimens were taken at altitudes of 30-1295 m; at rotting lemons; at mercury vapor and u-v light; in tropical seasonal forest; in tropical lowland forest. In Panamá specimens were taken at light; in glass fruitfly traps. Specimens were taken in blacklight traps in Puerto Rico. The single specimen from Florida was taken in a Malaise/flight intercept trap in a pineland forest.

Geographical distribution (Map 12).-- This species ranges through Lower and Nuclear Central America to both the Gulf and Pacific Versants of México, between the Tropic of Cancer and the Isthmus of Tehuantepec, and eastward to the Greater Antillean islands of Puerto Rico, Hispaniola, Jamaica and Cuba, and northward to the southern tip of Florida. The isolated occurrence of this species near Belém, Brazil, might be the result of an accidental importation there through shipping.

Chorological affinities.-- The range of this species overlaps those of *C. poecila*, *C. foveolata*, and *C. cupreotincta* in Middle America.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of the *C. foveolata* - *C. teutonica* lineage.

Material examined.-- A total of 127 specimens, including types, were examined. Non-type material was seen from the following localities:

BRAZIL Para. Belem (USNM)(ZSMM); Bôa, Vista Mu. Castanhal (USNM). Collections in October and January.

COSTA RICA Guanacaste. 3 km n Canas, Itac. La Pacifica (UASM); 4 km nw Canas, La Pacifica (CNC); **Limón**. Las Mercedes (USNM). Collections in April and June.

CUBA Las Villas. Soledad (Cienfuegos) (MCZ); Trinidad Mts. (MCZ)(MNHP); **Oriente**. Gran Piedra Rge. (MCZ); Rio Frio, Boniato Rge. (BMNH)(MCZ). Collections in May, June, and October.

GUATEMALA Petén. Tikal (FSCA). Collection in July.

HAITI Artibonite. Ennery (BMNH)(MCZ). Collection in August.

JAMAICA Surrey. St. Andrew. 136 Barbican Road (street address in Kingston)(JAMU); Irish Town (JAMU)(MCZ); St. Thomas. Bath (FSCA). Collections in July and October.

MÉXICO (IZWP); **Campeche**. Chicana ruins, 9.7 km e Xpujil (UASM); **Chiapas**. Chorreadera St. Pk. (LSUC); 1.4 km n Frontera Comalapa (UASM); Bonampak Rd., 100 km se Palenque (UASM); **Nayarit**. 37 km se Tepic (UASM); **Oaxaca**. 0.8 km e Tapanatepec, Rte. 190 (UASM); 10.5 km s Valle Nacional (UASM); **San Luis Potosí**. El Salto Falls, 12 km nw El Naranjo (SEMC); **Veracruz**. 33 km ne Catemaco, Los Tuxtla Biol. Stn. (UASM); Los Tuxtlas Biol. Stn., ca. 32.2 km e Catemaco (UASM); Los Tuxtla Biol. Station (UASM); Mirador (BMNH); Tebanca (UASM). Collections in May to August.

PANAMA (ZSMM); **Canal Zone**. Barro Colorado Is. (USNM); Panamá. El Cermeno (USNM); La Campana (USMN); Las Cumbres (OSUC); Taboga Island (BMNH). Collections in April to July, and September to December.

PUERTO RICO Rd. 10, Km. 24 (JMPR). Collections in June and September.

UNITED STATES Florida. Dade Co. Camp Mahachee, nr. Matheson Hammock (FSCA); Everglades N.P., Long Pine Key (SPC). Collections were made in July to September and December.

Coptodera foveolata, new species

Figs. 23G, 24I & 24J; Map 12

Type material.-- HOLOTYPE male, labelled: MEXICO. Vera Cruz Tebanca. ex. foliage, fallen tree. 27.vi.1985 Askevold & Heffern [USNM]. ALLOTYPE female, labelled same as holotype [USNM]. 1 male PARATYPE, labelled same as holotype [UASM].

Type locality.-- Tebanca, state of Veracruz, México.

Derivation of specific epithet.-- From Latin *fovea*, in allusion to the large setigerous foveae on the disc of each elytron.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head brunneous; pronotum rufo-brunneous to brunneous with broad testaceous lateral margins; elytra brunneous to rufo-piceous with testaceous markings; lateral margin of elytra testaceous to rufo-testaceous; appendages, antennae, and mouthparts brunneo-testaceous to rufo-testaceous, tibiae and tarsomeres darkened. Dorsal surface with moderate green lustre. Ventral surface testaceous with thoracic sterna brunneo-testaceous to brunneous (epipleuron not darkened at shoulder).

Elytra (Figs. 23G). Discal setae set in foveate punctures; interneurs finely punctate.

Male genitalia. As in Figs. 24I-24J, median lobe with membranous portion medium-long; apical portion medium-short, in lateral aspect slender, rod-like, hardly tapered, in dorsal aspect broader; apex in lateral aspect narrowly rounded, in dorsal aspect, more broadly so. Internal sac spine A absent; spine group B with one spine of medium size; spine group C with two medium-short spines.

Notes about habitat.-- All specimens were taken from foliage in a fallen tree and on vegetation.

Geographical distribution (Map 12).-- This species is known only from the Gulf Versant of México, between the Tropic of Cancer and the Isthmus of Tehuantepec.

Chorological affinities.-- *C. foveolata* and its adelphotaxon, *C. nigroviridis* - *C. teutonica*, are allopatric, but the ranges of this species and *C. nigroviridis* may overlap.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of the *C. nigroviridis* - *C. teutonica* lineage.

Material examined.-- Type material only; see above for details.

Coptodera nigroviridis, new species

Figs. 23H, 24K & 24L; Map 12

Type material.-- HOLOTYPE male, labelled: MEXICO, Chiapas, Pq. Montebello, Laguna Pojoj, 12.VI.1989.H.Howden [USNM]. ALLOTYPE female, labelled: MEX. Hidalgo Rte.105, 3.2km.n. Tlanchinol 1540m. in vegetation June 23. 1975; MEX. EXP. 1975 G.E. Ball & H.E. Frania collectors [USNM].

Type locality.-- Parque Montebello, state of Chiapas, México.

Derivation of specific epithet.-- From Latin *niger* and *viridis*, in allusion to the dark, black-green color of this species.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head brunneous to rufo-piceous; pronotum brunneous to rufo-piceous with broad testaceous lateral margins; elytra brunneous to rufo-piceous with testaceous markings; lateral margin of elytra testaceous; antennae testaceous to rufo-brunneous; mouthparts brunneo-testaceous to rufo-piceous; appendages brunneo-testaceous to rufo-brunneous, tibiae and tarsomeres darkened, brunneous to nearly rufo-piceous. Dorsal surface with moderate green lustre. Ventral surface testaceous to brunneous with thoracic sterna brunneo-testaceous to dark brunneous (epipleuron not darkened at shoulder), sterna 4 to 6 rufo-piceous at lateral edge.

Elytra (Fig. 23H). Discal setae set in foveate punctures; interneurs finely punctate.

Male genitalia. As in Figs. 24K-24L, median lobe with membranous portion medium; apical portion medium, in lateral aspect triangular, tapered gradually, in dorsal aspect slender, parallel-sided; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A absent; spine group B with two long spines; spine group C with two long spines.

Notes about habitat.-- The allotype was collected in cloud forest on bark of a dead standing tree at 1540 m altitude.

Geographical distribution (Map 12).-- This species is known only from México: north of the Isthmus of Tehuantepec on the Gulf Versant; and south of the Isthmus on the Pacific Versant.

Chorological affinities.-- The range of this species overlaps the range of its near relative, *C. foveolata*, on the Atlantic Versant of México. However, the range of *C. nigroviridis* and its adelphotaxon, *C. rufescens* + *C. teutonica*, are separated widely.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of the species pair *C. rufescens* + *C. teutonica*.

Material examined.-- Type material only; see above for details.

Coptodera rufescens Buquet
Figs. 12I-12L, 23I, 24M & 24N; Map 12

Coptodera rufescens Buquet 1835: 617. Type material: not seen. Type locality: Cayenne, French Guiana.-- Chaudoir, 1869: 172.

Coptodera luteopicta Chaudoir 1850: 363. Type material: LECTOTYPE female, labelled: luteopicta type Chaud (handwritten); Ex Musaeo Chaudoir (red print); rufescens Buquet Bresil Novofrib Schaum (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Novofriburgo, Rio de Janeiro, Brazil.-- Chaudoir 1869: 172.

Note about synonymy.-- Even though we have not seen the type of *C. rufescens*, we accept Chaudoir's synonymy of *C. luteopicta*.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head rufo-testaceous; pronotum bicolored, testaceous with rufous marking each side of median line; elytra rufous to rufo-brunneous with testaceous markings; lateral margin of elytron testaceous to rufo-testaceous; antennae and mouthparts rufo-testaceous to rufous; femora testaceous, darkened apically; tibiae and tarsi rufous to rufo-brunneous, tibiae darkened laterally. Ventral surface testaceous to rufo-testaceous; metepisternum rufous.

Elytra (Fig. 23I). Interneurs finely punctate.

Legs. Tarsal claws long, finely denticulate in basal half.

Male genitalia. As in Figs. 24M-24N, median lobe with membranous portion medium-short; apical portion medium-long, in lateral aspect trianguloid, narrowed gradually toward apex, in dorsal aspect widened, spatulate; apex in lateral aspect narrowly rounded, in dorsal aspect broadly rounded. Internal sac spine A absent; spine group B with three thick, moderately long spines; spine group C with single thick, moderately long spine.

Ovipositor. Stylomere 2 as in Figs. 12I-12L.

Notes about habitat.-- None available.

Geographical distribution (Map 12).-- This species is known from the Southern Atlantic zone of Brazil, and from French Guiana, in South America.

Chorological affinities.-- One of the known localities for this species is close to the single locality for its adelphotaxon, *C. teutonica*. The two species may be sympatric, at least in part of their range.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. teutonica.*

Material examined.-- We examined 3 specimens, including types, and saw non-type material from the following localities:
BRAZIL (IZWP); **Rio Grande do Sul**. Rio Grande (IZWP).

Coptodera teutonica, new species

Figs. 7D, 23J, 24O & 24P; Map 12

Type material.-- HOLOTYPE, male labelled: BRAZIL,Santa Cata- rina,Nova Teutonia I-1977 Fritz Plaumann Cal.Acad.Sci.Coll. [CAS].

Type locality.-- Nova Teutonia, state of Santa Catarina, Brazil.

Derivation of specific epithet.-- From "Teutonia" of Nova Teutonia, the type locality.

Description.-- Character states of the *C. festiva* group and the following. See Tables II, IV and VI for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head dark brunneous medially, rufo-testaceous laterally; pronotum bicolored, broad brunneous macula each side of dark testaceous marking along midline, markedly broad testaceous lateral margins, anterior and posterior margins testaceous; elytra rufo-piceous to brunneous near apex, with testaceous markings; lateral margin of elytron testaceous; antennae and mouthparts testaceous; femora and tibiae testaceous, femora darkened at apex, tibiae darkened medially; tarsi rufo-testaceous. Dark markings on dorsal surface of head and pronotum with faint green lustre; dark markings of elytra with moderate green lustre. Ventral surface testaceous, abdominal sterna 1-3 darkened laterally, thoracic sterna brunneous (elytral epipleuron brunneous).

Pronotum. As in Fig. 7D.

Elytra (Fig. 23J). Interneurs punctate.

Male genitalia. Median lobe as in Figs. 24O-24P, membranous portion medium-short; apical portion medium, in lateral aspect nearly parallel, tapered gradually toward apex, in dorsal aspect rod-like, sides parallel; apex in lateral aspect narrowly rounded, in dorsal aspect moderately broadly rounded. Internal sac spine A absent; spine groups B and C with two large spines each.

Notes about habitat.-- No information is available.

Geographical distribution (Map 12).-- This species is known only from the type locality in the Southern Atlantic zone of Brazil.

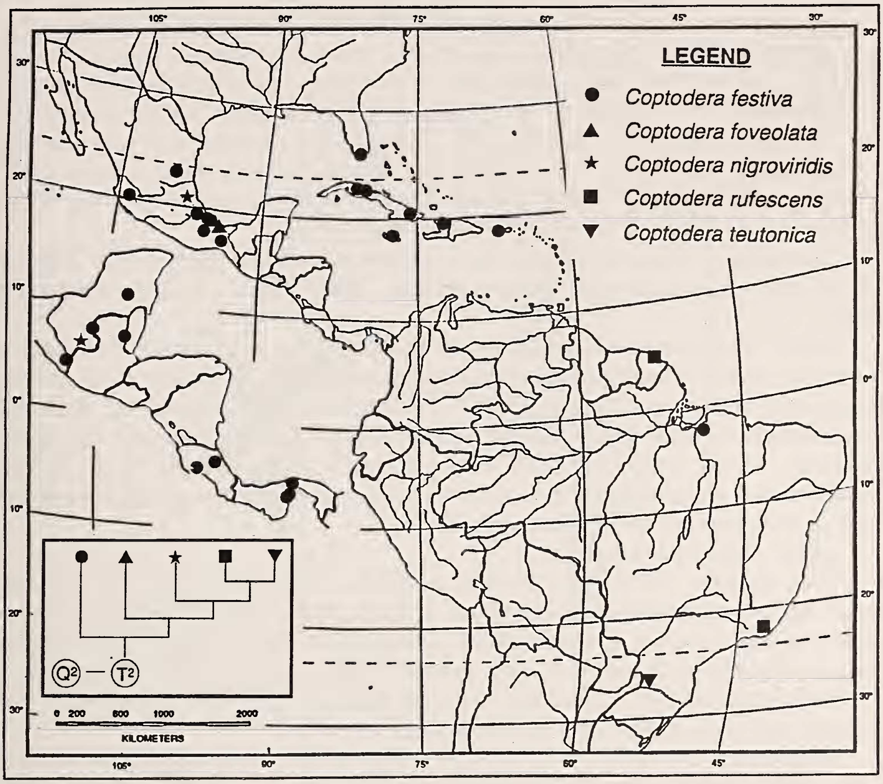
Chorological affinities.-- This species and its adelphotaxon, *C. rufescens*, may be sympatric, since both occur in the Southern Atlantic zone of Brazil.

Phylogenetic relationships (Fig. 36).-- See the topic for *C. rufescens* above, the adelphotaxon of *C. teutonica.*

Material examined.-- Type material only, see above for details.

Coptodera aeneorufa **Group**

This group has a single species with the character states of the *C. festiva* group, except the labrum is slightly wider than long and the elytra are unicolorous. See Table I for features of mandibles. Male genitalia with median lobe pleuropic-left; membranous portion medium-long; internal sac with macrospines (Figs. 25A-25B). Ovipositor with ensiform setae of stylomere 2 on



MAP 12. Geographical distribution of *Coptodera festiva* Dejean, *C. foveolata*, new species, *C. nigroviridis*, new species, *C. rufescens* Buquet and *C. teutonica*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

dorsal margin (cf. Fig. 12I); nematiform setae present. The geographical range of this group includes the Amazon Basin and Surinam in South America.

Chorological affinities.-- The geographical range of the *C. aeneorufa* group is broadly overlapped by the combined ranges of its adelphotaxa, the *C. bifasciata*, *C. emarginata*, *C. picea* and *C. aerata* groups (Maps 13-20).

Phylogenetic relationships (Fig. 35).-- The *C. aeneorufa* group is the adelphotaxon of the *C. bifasciata* - *C. aerata* group lineage.

Coptodera aeneorufa Bates
Figs. 25A & 25B; Map 13

Coptodera aeneorufa Bates 1869: 76. Type material: LECTOTYPE (here selected) male, labelled: Ega (handwritten); TYPE (red paper); aeneorufa Bates (handwritten); chalcoptera Chaud (handwritten); Ex Musaeo H.W. Bates 1892; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- 1870: XVI.

Coptodera chalcoptera Chaudoir 1869: 184. Type material: LECTOTYPE (here selected) male, labelled: LECTO (red paper); TYPE (red paper); ♂; Ex Musaeo Chaudoir; chalcoptera Chaud; Coptodera chalcoptera Chaud det. G.E. Ball '87; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (Tefé), Amazonas, Brazil.-- Bates 1870: XVI.

Note about synonymy.-- Based on study of type material, we confirm the synonymy proposed by Bates, of the names *C. aeneorufa* and *C. chalcoptera.*

Description.-- Character states of the *C. aeneorufa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head brunneo-testaceous to rufo-brunneous; pronotum brunneo-testaceous to rufo-brunneous, with a rufo-brunneous to brunneous spot each side of mid-line; elytra dark brunneo-testaceous to brunneous, with faint greenish to aeneous lustre; lateral margins of elytra testaceous to rufo-testaceous; appendages, antennae, and mouthparts testaceous to brunneo-testaceous, tibiae darkened. Ventral surface testaceous to brunneo-testaceous except proepisternum (medially), mesepisternum, mesepimeron, metasternum (laterally), metepisternum, and epipleuron at shoulder brunneo-testaceous to rufo-brunneous.

Elytra. Interneurs impunctate.

Male genitalia. As in Figs. 25A-25B, median lobe with apical portion medium, in lateral aspect trianguloid, tapered gradually toward apex, in dorsal aspect, trianguloid; apex in lateral aspect narrowly rounded, in dorsal aspect, pointed, apex bent to right. Internal sac spine A elongate; spine group B with three large spines; spine group C with single large spine.

Notes about habitat.-- Specimens were taken in primary (lowland tropical evergreen) forest in Brazil and in cis-Andean Peru on tree trunks, along a trail.

Geographical distribution (Map 13).-- The range of this species includes the Amazon Basin and Surinam in South America.

Chorological affinities and phylogenetic relationships.-- See these topics for the *C. aeneorufa* group, above.

Material examined.-- We examined 34 specimens, including types, and saw non-type material from the following localities:

BOLIVIA La Paz. Coroico (IZWP); Tumupasa (USNM). Collection was made in December.

BRAZIL Amazon (BMNH); Amazons (BMNH); **Amazonas**. 5 km w Alvaraes (CMNH); Ega (BMNH)(MNHP); **Para**. (CMNH)(MNHP); Belem (ZSMM); Bragance (MNHP); Santarem (MNHP). Collections were made in June, October, and February.

ECUADOR Napo Pastaza. 30 km e Lago Agrio, Via a Tarapoa (USNM). Collection was made in October.

PERU Huánuco. Monzon Valley, Tingo Maria (CAS); **Madre de Dios**. Pakitza, 12°07'S 70°58'W (USNM). Collections were made in October and November.

SURINAM Inini. Saül (ZSMM). Collection was made in March.

Coptodera bifasciata Group

This group has four species with character states of the *C. festiva* group, except the labrum is as wide as long to slightly wider than long. See Table I for features of mandibles. Male genitalia with median lobe pleuropic-right; membranous portion various degrees of "medium";

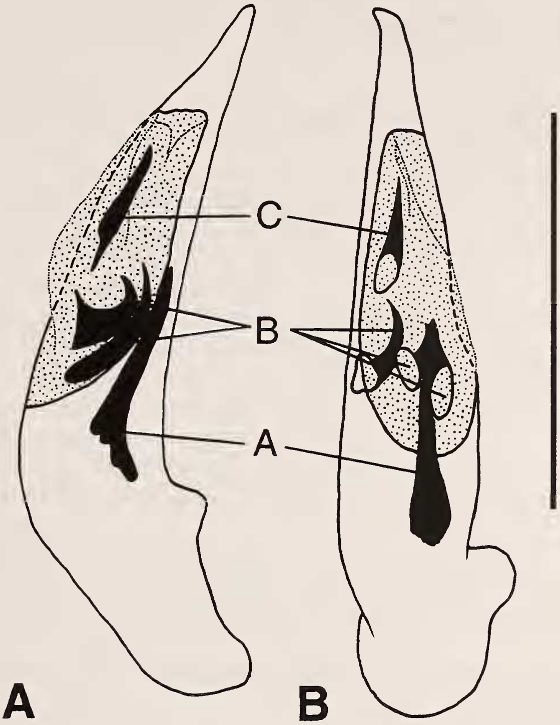
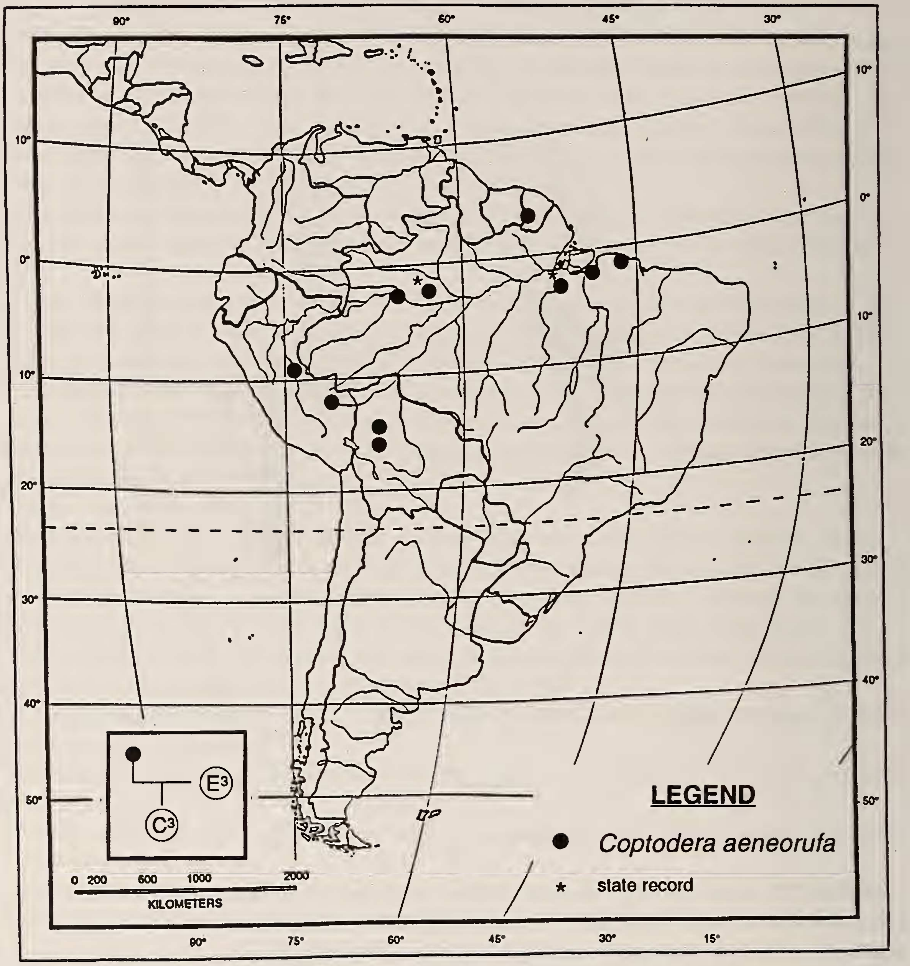


FIGURE 25. Line drawings of male genitalia of *C. aeneorufa* Bates. Fig. A left lateral aspect. Fig. B dorsal aspect. Scale bars = 1 mm. Legend: A, spine A; B, spine B; C, spine C.

internal sac with macrospines (Figs. 27A-27H). The geographical range of this group extends from the Southern Atlantic zone of South America, north through the Amazon Basin, and Lower and Nuclear Central America to the Gulf Versant of México north of the Isthmus of Tehuantepec (Map 14).

Chorological affinities.-- The geographical range of the *C. bifasciata* group is broadly overlapped by the combined ranges of its relatives, the *C. emarginata* + *C. picea* + *C. aerata* groups (Maps 14-20).

Phylogenetic relationships (Fig. 35).-- The *C. bifasciata* group is the postulated adelphotaxon of the *C. emarginata* group.



MAP 13. Geographical distribution of *Coptodera aeneorufa* Bates. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

Coptodera bifasciata Putzeys
Figs. 26A, 27A & 27B; Map 14

Coptodera bifasciata Putzeys 1845: 394. Type Material: HOLOTYPE female, labelled: type (hand written); Ex Musaeo Chaudoir (red print); TYPE (red paper); bifasciata Putzeys Brésil C.

Lacordaire Bonvouloir (box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Brazil.-- Chaudoir 1869: 180.

Description.-- Character states of the *C. bifasciata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous, darkened narrowly to broadly medially; pronotum bicolored, brunneous to rufo-piceous with broad testaceous lateral margins; elytra brunneous to rufo-piceous, with testaceous markings; lateral margins of elytra testaceous; appendages, antennae, and mouthparts testaceous to brunneo-testaceous. Dorsal surface with faint greenish to aeneous lustre. Ventral surface testaceous except proepisternum (medially to totally), mesepisternum, mesepimeron, metasternum (laterally), metepisternum, and epipleuron at shoulder rufo-brunneous to brunneous.

Elytra (Fig. 26A). Interneurs impunctate.

Male genitalia. As in Figs. 27A-27B, median lobe with membranous portion medium; apical portion medium, more or less flattened, in lateral aspect trianguloid, tapered gradually toward apex, in dorsal aspect narrow, rod-like, sides more or less parallel; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A long; spine group B with one long spine; spine group C with two spines of medium length.

Notes about habitat.-- No information is available.

Geographical distribution (Map 14).-- This species is recorded only from the Southern Atlantic zone of eastern Brazil.

Chorological affinities.-- The range of this species is overlapped by those of the other three species which are part of the *C. bifasciata* - *C. braziliensis* lineage.

Phylogenetic relationships (Fig. 36).-- This species is part of an unresolved trichotomy with *C. tripartita* and the *C. cupreotincta* + *C. braziliensis* lineage.

Material examined.-- We examined 9 specimens, including types, and saw non-type material from the following localities:

BRAZIL (BMNH); **Minas Gerais**. Caraça (MNHP); Rio Piracicaba (MNHP); **Santa Catarina**. (BMNH); **São Paulo**. Peruhybe (IZWP). Collection in February.

Coptodera tripartita Chaudoir
Figs. 26B, 27C & 27D; Map 14

Coptodera tripartita Chaudoir 1869: 180. Type material: LECTOTYPE (here selected) male, labelled: (blue rectangle); Ex Musaeo Chaudoir (red print); TYPE (red paper); tripartita Chaud Amazone Ega Bates (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.

Description.-- Character states of the *C. bifasciata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous, darkened narrowly to broadly medially; pronotum bicolored, brunneous to rufo-piceous with broad testaceous lateral margins, one dark spot each side of medial line; elytra brunneous to rufo-piceous, with testaceous markings; lateral margins of elytra testaceous; appendages, antennae, and mouthparts testaceous to brunneo-testaceous. Dorsal surface with faint greenish to aeneous lustre. Ventral surface testaceous except proepisternum (medially to totally), mesepisternum, mesepimeron, metasternum (laterally), metepisternum, and epipleuron at shoulder rufo-brunneous to brunneous.

Elytra (Fig. 26B). Interneurs impunctate.

Male genitalia. As in Figs. 27C-27D, median lobe with membranous portion medium-short; apical portion long, more or less flattened, in lateral aspect trianguloid, curved ventrad, in dorsal aspect slender, constricted slightly preapically; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A long; spine group B two long spines; spine group C two spines, medium length.

Notes about habitat.-- Specimens were taken in a primary (lowland tropical evergreen) forest in Brazil. In Venezuela, specimens were taken by Malaise trap in a rainforest at an altitude of 140 m.

Geographical distribution (Map 14).-- This species is recorded from the Southern Atlantic zone and Amazon Basin regions of cis-Andean Bolivia, Brazil, and Venezuela.

Chorological affinities.-- The range of this species is overlapped by those of the other three species which are part of the *C. bifasciata* - *C. braziliensis* lineage.

Phylogenetic relationships (Fig. 36).-- Based on type of median lobe (anopic-pleuropic[right]), this species is part of an unresolved trichotomy, including *C. bifasciata* and *C. cupreotincta* + *C. braziliensis* lineages.

Material examined.-- We examined 32 specimens, including types, and saw non-type material from the following localities:

BOLIVIA Cochabamba. (MNHP); **La Paz**. Tumupasa (USNM). Collection was made in December.

BRAZIL (BMNH); **Amazonas**. 5 km w Alvaraes (CMNH); Ega (MNHP); Forte Boa (IZWP); 30 km w Itaquatiara, Rio Urubu (CMNH); São Paulo de Olivença (MNHP); **Mato Grosso**. Chapada (=Chapada dos Guimaraes)(CMNH); **Para**. (BMNH); Monte Alegre (AMNH); Santarem (AMNH)(BMNH)(CMNH); Tapajos (MNHP). Collections were made in September to February.

PERU Loreto. Aguaitia (MPEG). Collection in September.

VENEZUELA Amazonas. Cerro de Neblina basecamp 0°50'N66°10'W (USNM). Collection was made in February.

Coptodera cupreotincta Bates
Figs. 26C, 27E & 27F; Map 14

Coptodera cupreotincta Bates 1869: 73. Type material: LECTOTYPE (here selected) male, labelled: ♂; TYPE; amazonica Chaud; cupreotincta Bates ♂ Ega; Ex Musaeo H.W. Bates 1892; LECTOTYPE Coptodera amazonica Bts By Erwin '76; Museum Paris ex Coll R. Oberthür [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- 1883: 183.

Coptodera tesselatus Chaudoir 1869: 199. NEW SYNONYMY. Type material: LECTOTYPE (here selected) male, labelled: Mexico Klgh (handwritten); Ex Musaeo Chaudoir (red print); tesselata Chaud Mexique Dr Haag-Rntenb (original box label); LECTO- TYPE (disc with purple border); LECTOTYPE Coptodera tesselata Chaud det. George E. Ball '72; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: México.

Coptodera amazonica Chaudoir 1869: 200. Type material: LECTOTYPE (here selected) male, labelled: (green rectangle); amazonica Chaud; Ex Musaeo Chaudoir; LECTO- TYPE (disc); LECTOTYPE Coptodera amazonica Chaud det. George E. Ball '72; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- Bates 1870: XVI.

Notes about synonymy.-- Chaudoir's *C. tesselatus* was based on specimens from Mexico, which is the northern limits of *C. cupreotincta*. The two are identical, and we believe them to be conspecific. Based on study of type material, we confirm the synonymy proposed by Bates, of the names *C. cupreotincta* and *C. amazonica.*

Comparisons.-- Males of *C. braziliensis* also have adhesive vestiture on tarsomeres 2 and 3 of the mid-leg.

Description.-- Character states of the *C. bifasciata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous, darkening medially; pronotum bicolored, brunneous with broad testaceous lateral margins; elytra dark brunneous with testaceous markings; lateral margin of elytra testaceous; appendages, antennae, and mouthparts testaceous; femora and tibiae darkened slightly medially. Dorsal surface with faint greenish to aeneous lustre. Ventral surface testaceous except mesepisternum, mesepimeron, metepimeron, and epipleuron at shoulder brunneo-testaceous to brunneous.

Elytra (Fig. 26C). Interneurs punctate.

Legs. Tarsomeres 2 and 3 of mid-leg of male with adhesive vestiture.

Male genitalia. As in Figs. 27E-27F, median lobe with membranous portion medium; apical portion medium, flattened, in lateral aspect trianguloid, tapered gradually toward apex, in dorsal aspect slender, sinuate; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A long; spine group B with one long spine; spine group C with two spines of medium size.

Notes about habitat.-- In Costa Rica, specimens were taken at an altitude of 100 m; on dry wood at night. In México specimens were taken at altitudes of 121-731 m; at black light. In Panamá specimens were taken at altitudes of 243-671 m; at lights; running on underside of elevated log; on log. In Peru specimens were taken at altitudes of 290-840 m; at white and u-v light, and on trees and logs at night.

Geographical distribution (Map 14).-- This species ranges from the Amazon Basin and Southern Atlantic zone of Brazil north through Lower and Nuclear Central America to México north of the Isthmus of Tehuantepec, on the Gulf Versant.

Chorological affinities.-- The known ranges of *C. cupreotincta* and its adelphotaxon, *C. braziliensis*, do not quite meet, but these species are probably sympatric in the Southern Atlantic zone of Brazil.

Phylogenetic relationships (Fig. 36).-- Based on similarities in male genitalia and males with adhesive vestiture on mid-tarsi, this species and *C. braziliensis* are postulated to be adelphotaxa.

Material examined.-- A total of 202 specimens, including types, were examined. Non-type material was seen from the following localities:

BOLIVIA Cochabamba. MNHP.

BRAZIL (MNHP); Amazon (BMNH); Amazons (BMNH); Amazones (BMNH); **Amazonas**. (HNHM)(IZWP); Ega (BMNH)(MNHP); **Bahia**. Cachimbo (MNHP); **Para**. (CMNH); Belem (ZSMM)(USNM); **Paraiba**. (MNHP); **Rio de Janeiro**. Rio de Jan. (CMNH); **São Paulo**. Rio Pardo (MNHP). Collections in June to August, October, and December.

COSTA RICA Limón. Hamburg farm, Reventazon (BMNH)(IZWP)(USNM); Las Mercedes (USNM); Ramal Parismina (USNM). Collections in March to June and October.

MÉXICO Chiapas. 4.9 mi n Frontera Comalapa (UASM); Palenque ruins (UASM); Portugal, 7 mi se Simojovel (UCBC); **Oaxaca**. 5.6 mi s Valle Nacional, Rte. 175 (UASM); **Veracruz**. Lake Catemaco (UASM). Collections in April to August.

NICARAGUA Chontales. (BMNH).

PANAMA Canal Zone. Barro Colorado (MCZ)(USNM); Madden Forest (USNM); Madden Forest 9°06'N79°36'W (USNM); Madden Forest, Mi. 2.5, 9°05'N79°37'W (USNM); **Chiriqui**. Bugaba

(BMNH)(MCZ)(MNHP)(USNM); David (BMNH); Volcan de Chiriqui (BMNH); **Panamá**. Altos de Maje (HPST); Bayano Dist., 31 km e Canita (RHTC); Pozo Azul, Finca Vega, nr Las Nubes (CAS). Collections in April to August.

PERU Cuzco. Quiroz, R. Paucartambo (MCZ); **Junín**. Sani Beni, 8 km e Satipo (SEMC); **Madre de Dios**. Pakitza, 11°55'48"S 71°35'18"W (USNM); Pakitza, 12°07'S 70°58'W (USNM); Rio Tambopata Reserve, 30 km (air) sw of Puerto Maldonado (BMNH)(DHK). Collections were made in September to November.

Coptodera braziliensis, new species

Figs. 26D, 27G & 27H; Map 14

Type material.-- HOLOTYPE male, labelled: Hansa Humboldt S. Cat. Braz. A. Maller (hand printed) [MCZ]. ALLOTYPE female, labelled: Nova Teutonia, Sta. Cat., Brazil 30 May 41 F. Plaumann [MCZ]. 7 PARATYPES, sex and label data as follows: 1 male: Cauna S.Cath.,Brazil Dec. 1948; A. Maller, Coll. Frank Johnson Donor [AMNH]. 1 male: Nova Teutonia Santa Catarina BRAZIL IX.21.52 Fritz Plaumann [MCZ]. 1 male: BRASILIEN Rio Grde.do Sul K.E.Hüdepohl; S.Francisco de Paula XI 1959; Coll. Hüdepohl Kat. Nr. 48/1980 [ZSMM]. 1 male: MUSEUM PARIS RIO DE CASTELNAU 1844 (green paper); green disc [MNHP]. 1 male: Brasilia; 792 27; undulata Brasil (HNHM). 1 female: MUSEUM PARIS MISIONES ENV. DE SAN-IGNACIO VILLA LUTECIA E.R. WAGNER 1910 (green paper); JUIN; SEPTEMBRE [MNHP]. 1 female: Bra. (hand printed); F.C. Bowditch Coll.; Coptodera, bifasciata, Ptz (hand written) [MCZ].

Type locality.-- Hansa Humboldt (=Corupá), state of Santa Catarina, Brazil.

Derivation of specific epithet.-- Latinized name of the country in which this species is found.

Description.-- Character states of the *C. bifasciata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum rufo-brunneous with faint to moderate green lustre; pronotum at times with diffusely paler lateral margins; elytra rufo-brunneous, with faint greenish to aeneous lustre, with testaceous markings; lateral margin of elytra rufo-testaceous; appendages, antennae, and mouthparts testaceous to rufo-testaceous. Ventral surface rufo-testaceous to brunneous.

Elytra (Fig. 26D). Interneurs finely punctulate.

Legs. Tarsomeres 2 and 3 of midleg of male with adhesive vestiture as in *C. cupreotincta*.

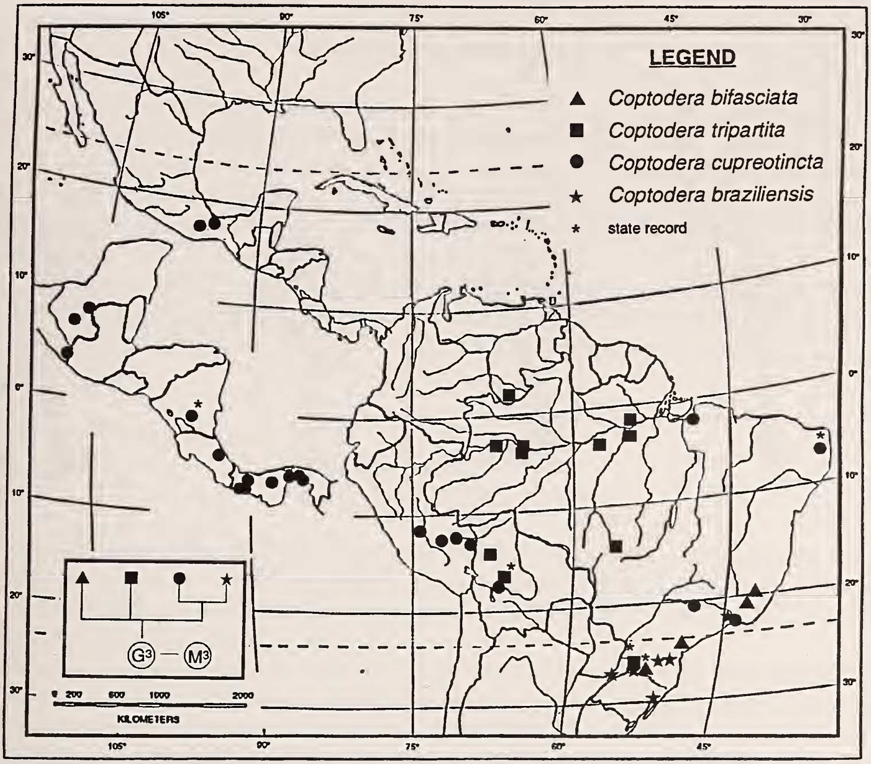
Male genitalia. As in Figs. 27G-27H, median lobe with membranous portion medium-long; apical portion medium-long, in lateral aspect trianguloid, tapered gradually toward apex, in dorsal aspect sinuate, rod-like; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A long; spine group B with three long spines; spine group C with one short spine.

Notes about habitat.-- None available.

Geographical distribution (Map 14).-- This species is known only from the Southern Atlantic zone of eastern Brazil and adjacent Argentina.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for *C. cupreotincta* above, the adelphotaxon of *C. braziliensis*.

Material examined.-- Type material only; see above for details.



MAP 14. Geographical distribution of *Coptodera bifasciata* Putzeys, *C. tripartita* Chaudoir, *C. cupreotincta* Bates and *C. braziliensis* new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

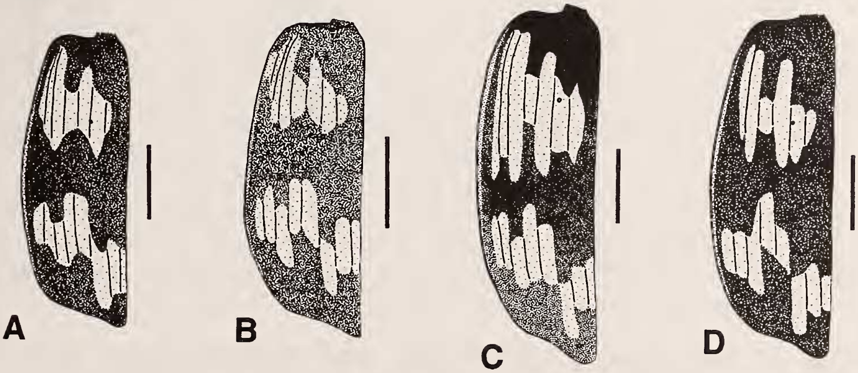


FIGURE 26. Line drawings of left elytron of *Coptodera bifasciata* group, dorsal aspect. Fig. A: *C. bifasciata* Putzeys. Fig. B. *C. tripartita* Chaudoir. Fig. C: *C. cupreotincta* Bates. Fig. D: *C. braziliensis* new species. Scale bars = 1 mm. Legend: A, spine A; B, spine B; C, spine C.

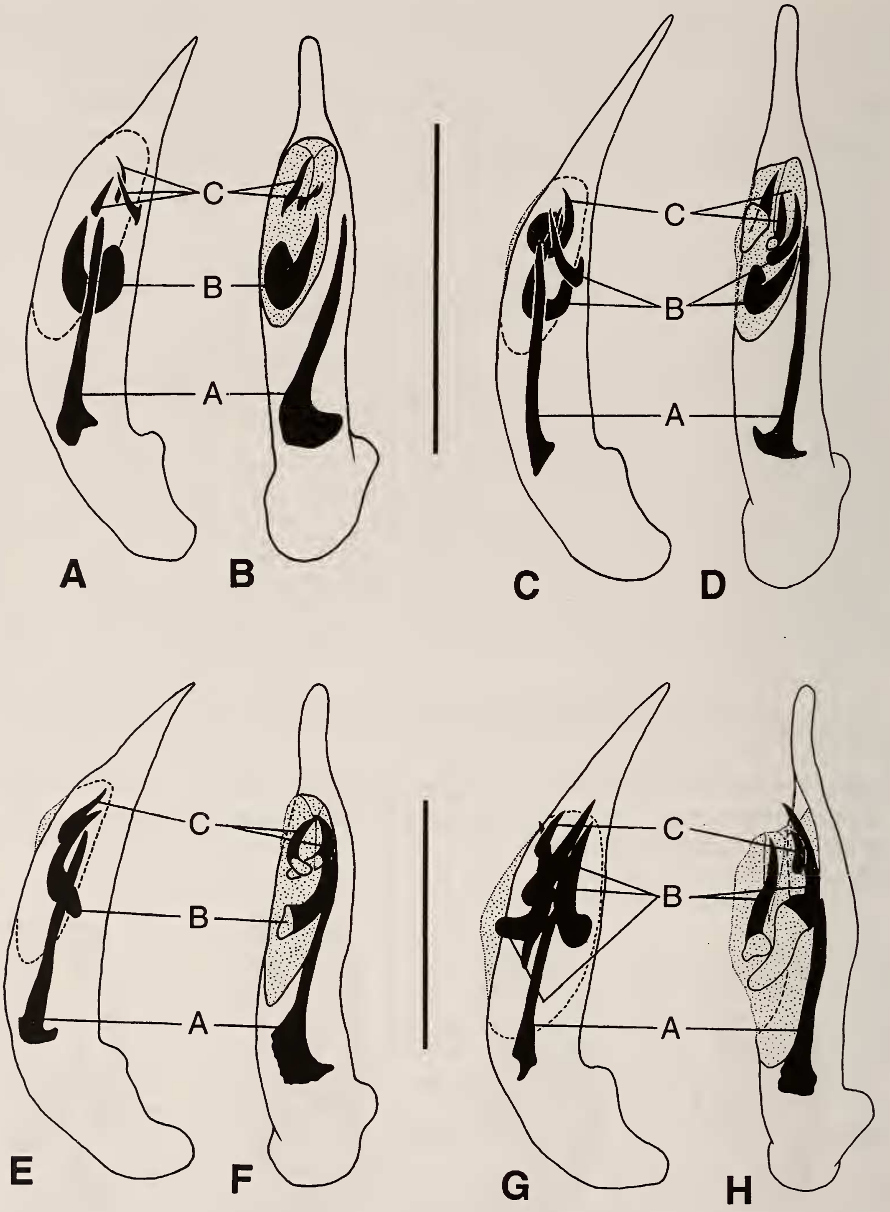


FIGURE 27. Line drawings of male genitalia of *Coptodera bifasciata* group. Figs. A, C, E & G left lateral aspect. Figs. B, D, F & H dorsal aspect. Figs. A-B: *C. bifasciata* Putzeys. Figs. C-D: *C. tripartita* Chaudoir. Figs. E-F: *C. cupreotincta* Bates. Figs. G-H: *C. braziliensis*, new species. Scale bars = 1 mm.

Coptodera emarginata Group

This group has three species with character states of the *C. festiva* group, except the anterior margin of the labrum (slightly wider than long) is more emarginate in some species (indicated in the species description), and the elytra are metallic and unicolorous rather than variegated. See Table I for features of mandibles. Male genitalia with median lobe anopic to pleuropic-right; membranous portion medium-long to long. The geographical range of this group extends from South America north through Central America into México.

Chorological affinities.-- The geographical range of the *C. emarginata* group is broadly overlapped by the combined ranges of its adelphotaxon, the *C. bifasciata* group (Map 14 and 15).

Phylogenetic relationships (Fig. 35).-- This group is the postulated adelphotaxon of the *C. bifasciata* group.

Coptodera chalcites Bates

Figs. 28A, 28C & 28D; Map 15

Coptodera chalcites Bates 1869: 75. Type material: LECTOTYPE (here selected) male, labelled: Ega (handwritten); TYPE (red paper); chalcites Bates ♂; Ex Musaeo H.W. Bates 1892; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), state of Amazonas, Brazil.-- 1870: XVI.

Coptodera aeneocuprea Chaudoir 1869: 177. Type material: LECTOTYPE (here selected) male, labelled: LECTO (red paper); TYPE (red paper); (green rectangle); aeneocuprea Chaud (handwritten); Ex Musaeo Chaudoir (red print); Coptodera aeneocuprea Chaud det. George E. Ball '87; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), state of Amazonas, Brazil.-- Bates 1870: XVI.

Note about synonymy.-- Based on study of type material, we confirm the synonymy proposed by Bates, of the names *C. chalcites* and *C. aeneocuprea.*

Description.-- Character states of the *C. emarginata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head, pronotum and elytra rufo-brunneous to dark brunneous; antennae and mouthparts rufous; appendages rufo-brunneous. Dorsal surface of elytra with faint to moderate green, aeneous or violaceous lustre, faint on the pronotum. Ventral surface rufo-brunneous.

Mouthparts. Anterior margin of labrum moderately emarginate medially.

Elytra. Interneurs punctate; apex with sutural angle broadly rounded (Fig. 28A).

Male genitalia. As in Figs. 28C-28D, median lobe with membranous portion medium, dorsal, anopic; membranous area partially sclerotized near apex. Apical portion medium-short, in lateral aspect trianguloid, slender, tapered gradually toward apex, in dorsal aspect broadly trianguloid, tapered gradually; apex in lateral aspect pointed, in dorsal aspect moderately rounded. Internal sac spine A absent; spine group B two medium size spines; spine group C two medium-small sized spines.

Notes about habitat.-- Specimens were taken in Ecuador at an altitude of 100 m; under bark of fresh cut tree and from the canopy of a fallen tree. In Peru, specimens were taken at altitudes of 200 and 290 m; at light, at white light, on logs and running on bark of a fallen dead tree.

Geographical distribution (Map 15).-- This species is recorded from cis-Andean South America in the western and central parts of the Amazon Basin.

Chorological affinities.-- The range of *C. chalcites* is overlapped by that of one of its relative, *C. acutipennis*.

Phylogenetic relationships (Fig. 36).-- This species is postulated to be the adelphotaxon of *C. emarginata* + *C. acutipennis*, based on form of the median lobe.

Material examined.-- We examined 42 specimens, including types, and saw non-type material from the following localities:

BRAZIL Amazons (BMNH); **Amazonas**. Ega (BMNH)(MNHP); Fonte Boa (BMNH); Tonantins (MNHP); **Para**. Santarem (CMNH)(IZWP).

COLOMBIA Amazonas. Leticia (CNC). Collection in July.

ECUADOR Napo Pastaza. Ashuara, on Rio Macuma, 10 km from Rio Morona (UASM); Limoncocha (HHES)(UASM). Collections were made in January, April, and July.

PERU Cuzco. Quiroz, R. Paucartambo (MCZ); **Junín**. Chanchamayo (MNHP); **Loreto**. Pebas (MNHP); **Madre de Dios**. Pakitza, 11°55'48"S 71°35'18"W (USNM); Pakitza, 12°07'S 70°58'W (USNM); 15 km ne Puerto Maldonado (SEMC); Rio Tambopata Reserve, 30 km (air) sw Puerto Maldonado, 12°50'S 69°20'W (DHK). Collections were made in June, July and September to November.

Coptodera emarginata Dejean
Figs. 28B, 28E & 28F; Map 15

Coptodera emarginata Dejean 1825: 276. Type material: HOLOTYPE male, labelled: emarginata m in Brazilia (Dejean's handwriting on green paper); Ex Musaeo Chaudoir (red print); TYPE (red paper); emarginata Dejean Bresil Coll Dejean (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Brazil.-- Chaudoir 1869: 175.

Lebia aenea Buquet 1834: 673. Type material: not seen. Type area: French Guiana.

Coptodera aenea: Chaudoir 1869: 175.

Note about synonymy.-- We accept Chaudoir's synonymy of *C. aenea*.

Description.-- Character states of the *C. emarginata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head, pronotum and elytra rufo-brunneous to dark brunneous; antennae and mouthparts brunneous; femora dark testaceous to rufo-brunneous, darkened apically; tibiae and tarsi brunneous. Dorsal surface of head and pronotum with moderate green lustre; elytra with moderate green lustre basally gradually fainter towards apex. Ventral surface brunneous; epipleuron dark testaceous.

Mouthparts. Anterior margin of labrum shallowly emarginate medially.

Elytra. Interneurs finely punctulate; apex with lateral and sutural angles spinose; apical margin sinuate before sutural angle (Fig. 28B).

Male genitalia. As in Figs. 28E-28F, median lobe with membranous portion long, lateral-right, pleuropic. Apical portion medium-long, more or less flattened, in lateral aspect broadest at base, abruptly narrowed, then sides parallel, in dorsal aspect rod-like; apex in lateral aspect very narrowly rounded, in dorsal aspect moderately broadly rounded. Internal sac spine A large; spine group B two large spines; spine group C one spine of moderate size.

Notes about habitat.-- None available.

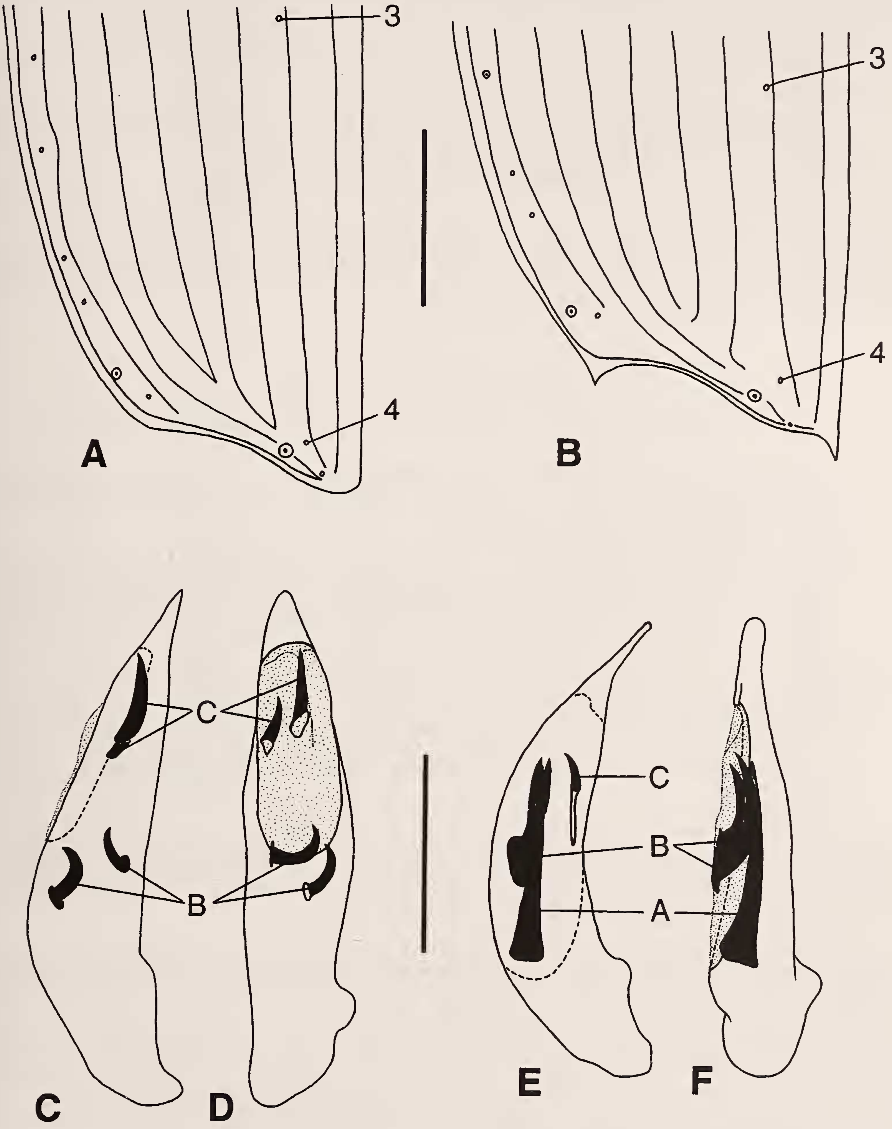


FIGURE 28. Line drawings of structures of *Coptodera emarginata* group. Figs. A-B apex of left elytron, dorsal aspect. Fig. A: *C. chalcites* Bates. Fig. B: *C. emarginata* Dejean. Figs. C & E and D & F male genitalia, left lateral and dorsal aspects respectively. Figs. C-D: *C. chalcites* Bates. Figs. E-F: *C. emarginata* Dejean. Scale bars = 1 mm. Legend: A, spine A; B, spine B; C, spine C; 3, discal setigerous puncture #3; 4, discal setigerous puncture #4.

Geographical distribution (Map 15).-- This species is known only from cis-Andean Brazil, south of the Amazon Basin, including the Southern Atlantic zone, and from Surinam in northeastern South America.

Chorological affinities.-- The geographical range of *C. emarginata* overlaps the range of its adelphotaxon, *C. acutipennis*, in Surinam.

Phylogenetic relationships (Fig. 36).-- Based on details of structure of the median lobe, *C. emarginata* is postulated to be the adelphotaxon of *C. acutipennis*.

Material examined.-- We examined 8 specimens, including types, and saw non-type material from the following localities:
BRAZIL (BMNH)(MNHP); **Goias**. Jatahy (BMNH); **Mato Grosso**. Chapada (=Chapada dos Guimaraes)(CMNH); **Minas Gerais**. Lambary (USNM); **São Paulo**. Riberão Prêto (MZSP). Collections were made in September and April.

Coptodera acutipennis (Buquet)

Figs. 1F, 6B, 6F, 11A-11D, 13B, 29A-29P, 30A-30L, 31A & 31B; Map 15

Lebia acutipennis Buquet 1834: 674. Type material: not seen. Type area: headwaters of the Oyapock River, French Guiana.-- Chaudoir, 1869: 176.-- Bates 1870: XVI; 1883: 181.

Coptodera acutipennis: Chaudoir 1869: 176.

Coptodera spinipennis Bates 1869: 75. Type material: LECTOTYPE (here selected) male, labelled: acutipennis Buq. sec. Chd.; spinipennis Bates Ega ♂; Ex Musaeo H.W. Bates 1892; Museum Paris ex Coll. R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- Bates 1870: XVI.

Coptodera scintillans Bates 1878: 604. NEW SYNONYMY. Type material: HOLOTYPE female, labelled: Chontales Nicaragua (handwritten [Bates']); scintillans Bates (handwritten [Bates']); W.W. Bates Biol Cent Amer; Lectotype ♀ Coptodera scintillans Bates By Erwin '76; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Chontales department, Nicaragua.

Note about synonymy.-- The new synonymy proposed above is based on comparison of type material of the two junior synonyms. The type material of *Lebia acutipennis* Buquet, to be expected in the Oberthür-Chaudoir collection (MNHP), is not there and evidently has been lost. We accept Bates' synonymy of *C. spinipennis*.

Description.-- Character states of the *C. emarginata* group and the following. See Tables VIII-X for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum brunneous to dark brunneous, with faint to moderate greenish to aeneous lustre; lateral margins of pronotum usually paler than pronotal disc; elytra brunneous to dark brunneous, with faint to very markedly developed greenish to aeneous lustre, lateral margins paler than elytral disc; antennae, mouthparts, and legs brunneo-testaceous to rufo-brunneous. Ventral surface brunneous to rufo-brunneous.

Mouthparts. Anterior margin of labrum shallowly emarginate to nearly straight (Fig. 1F); labium as in Figs. 6B & 6F.

Elytra. Interneurs finely punctate; apex with lateral angle sharply obtuse to spinose and sutural angles rectangular to spinose.

TABLE VIII. Variation in SBL among adults of *Coptodera acutipennis* (Buquet).

Morph	Country	N	Range	Mean
A[1]	México	1	8.83	8.83
B	México	2	8.58-9.25	8.92
C	México	2	8.33-8.42	8.38
D	Panamá	3	9.25-9.83	9.53
E	Ecuador	1	9.92	9.92
F	Peru	4	8.58-9.25	8.90
G	Peru	2	7.25-7.42	7.34
H	Bolivia	1	8.83	8.83
I	Ecuador	1	8.75	8.75
J	Bolivia	2	9.75- 9.92	9.84
J	Peru[2]	9	6.08- 7.83	6.83
J	Peru[3]	1	8.75	8.75
K	Brazil	4	9.17-10.00	9.71
K	Peru	1	8.33	8.33
L	Peru	1	7.58	7.58
M	Bolivia	1	8.25	8.25
N	Bolivia	2	8.92-9.17	9.05
-[4]	Panamá	2	6.67-7.00	6.84
-[5]	Peru	6	6.67-7.25	6.99
-	Bolivia	7	8.08-10.67	9.45
-	Panamá	8	9.50-10.08	9.78
-	México	3	8.00-10.00	8.99

[1] - alphabetical designations for males as described in text
[2] - state of Madre de Dios
[3] - state of Loreto
[4] - teneral males not dissected
[5] - sample of females from different countries (not all specimens included)

Male genitalia. As in Figs. 29A-29P, 30A-30L and 31A-31B, median lobe with membranous portion medium-long to long, dorsal, anopic to lateral-right, pleuropic. Apical portion various (for details, see below, under variation); apex in lateral aspect narrowly rounded, in dorsal aspect narrowly to moderately broadly rounded. Internal sac spine A large; spine group B absent; spine group C with one or two small to large spines (see also Figs. 11).

Female genitalia. Reproductive tract as in Fig. 13B.

Notes about variation.-- This species was very difficult to diagnose because of the variation in the male genitalia - not only the form of the median lobe, but also the number and location of spines on the internal sac. Externally, there are no visible characters to separate this complex into distinct species. Rather than name each subgroup (based on the different male genitalia) as a new species, we decided to use the designation of morphs. These designations were alphabetical, using letters A to N (Figs. 29A-29P and 30A-30L). All males were dissected except two specimens in MNHP (both from Ega, Brazil) and two extremely teneral specimens in USNM (both from Canal Zone, Panamá). Females were not grouped into these morphs, as it was not possible to associate

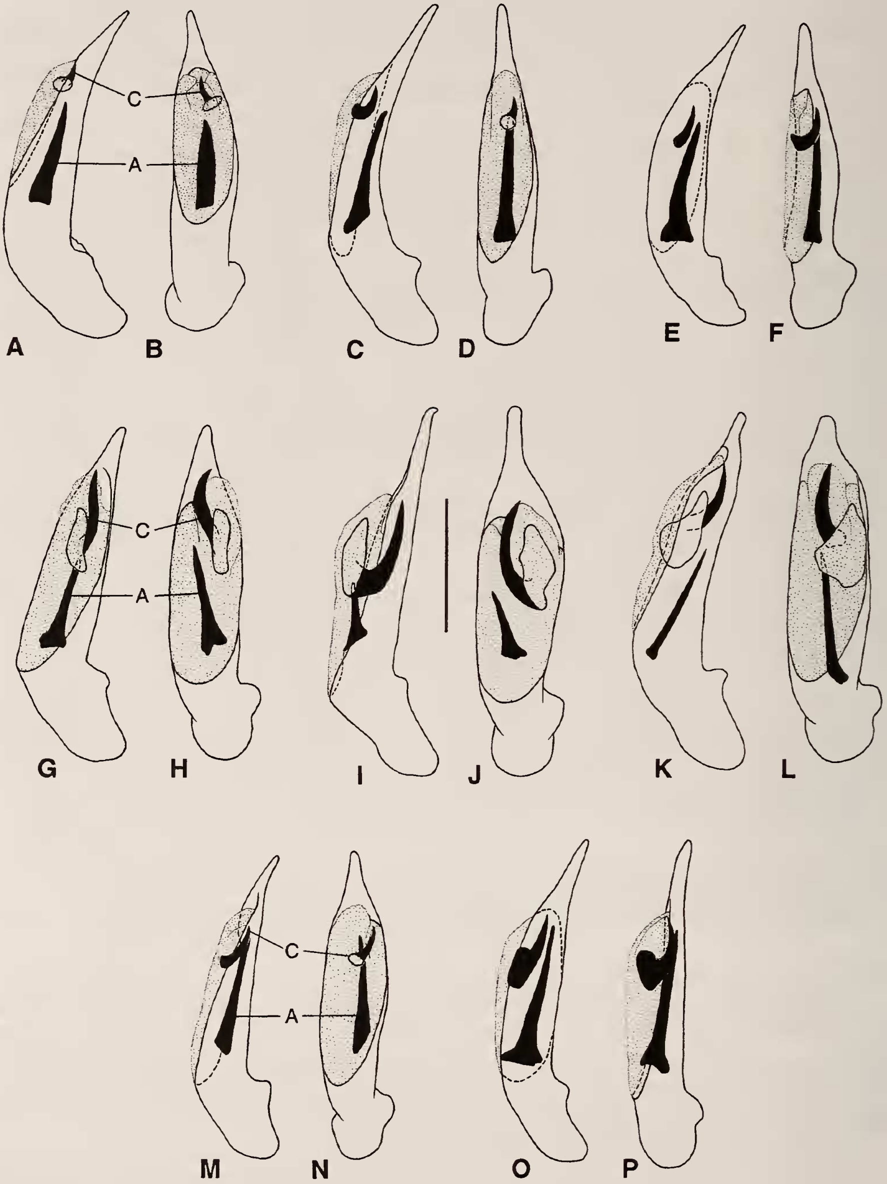


FIGURE 29. Line drawings of male genitalia of *C. acutipennis* (Buquet). Figs. A, C, E, G, I, K, M & O left lateral aspect. Figs. B, D, F, H, J, L, N & P dorsal aspect. Figs. A-B: morph A. Figs. C-D: morph B. Figs. E-F: morph C. Figs. G-H: morph D. Figs. I-J: morph E. Figs. K-L: morph F. Figs. M-N: morph G. Figs. O-P: morph H. Scale bars = 1 mm. Legend: A, spine A; C, spine C.

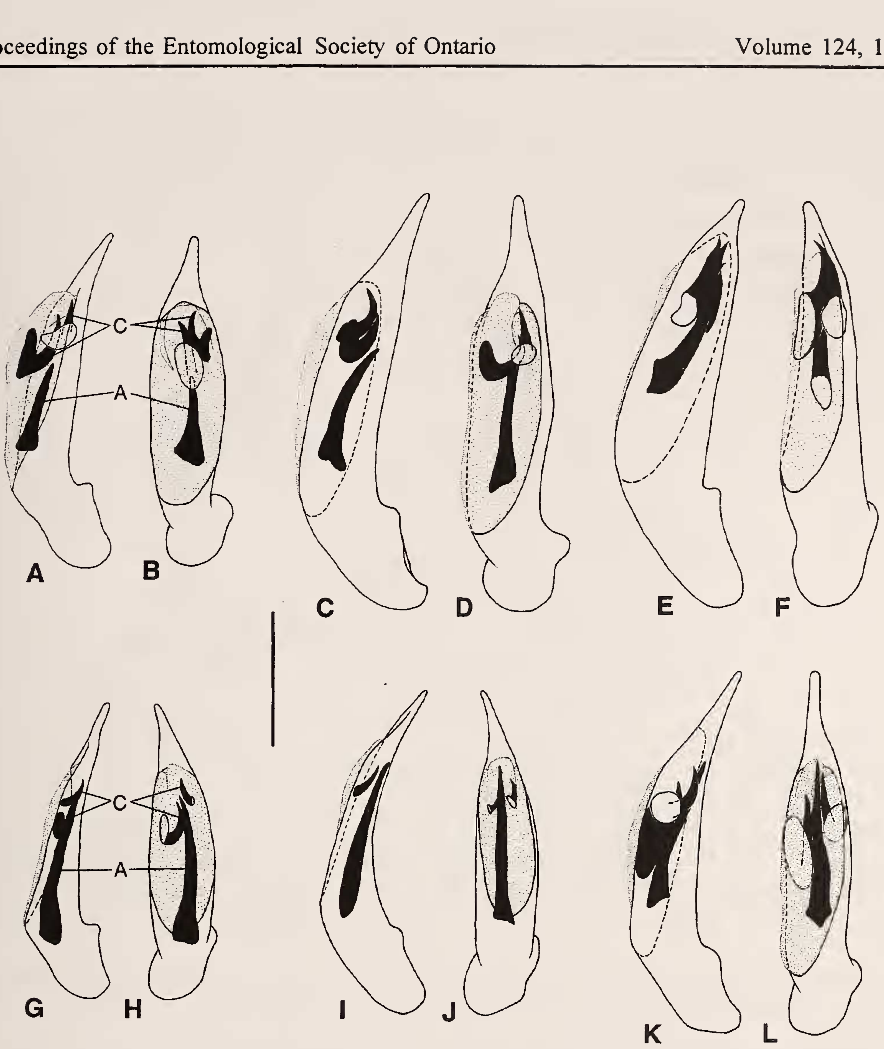


FIGURE 30. Line drawings of male genitalia of *C. acutipennis* (Buquet). Figs. A, C, E, G, I & K left lateral aspect. Figs. B, D, F, H, J & L dorsal aspect. Figs. A-B: morph I. Figs. C-D: morph J. Figs. E-F: morph K. Figs. G-H: morph L. Figs. I-J: morph M. Figs. K-L: morph N. Scale bars = 1 mm. Legend: A, spine A; C, spine C.

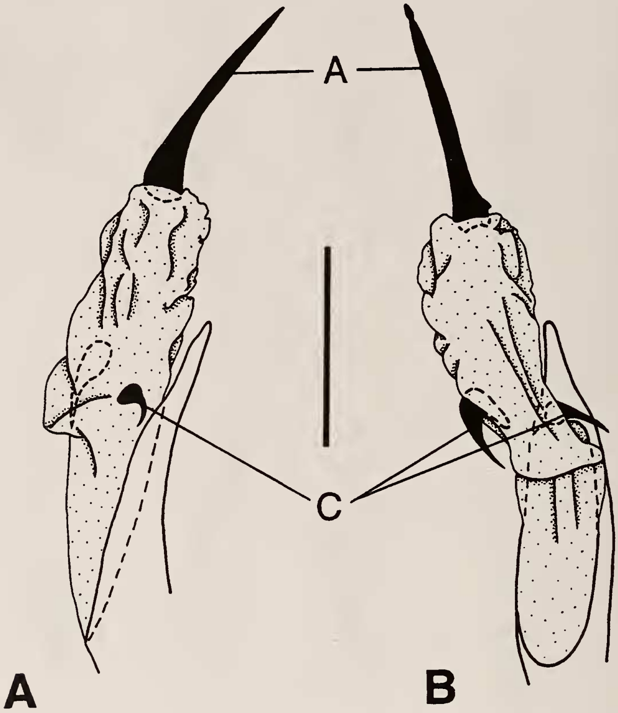
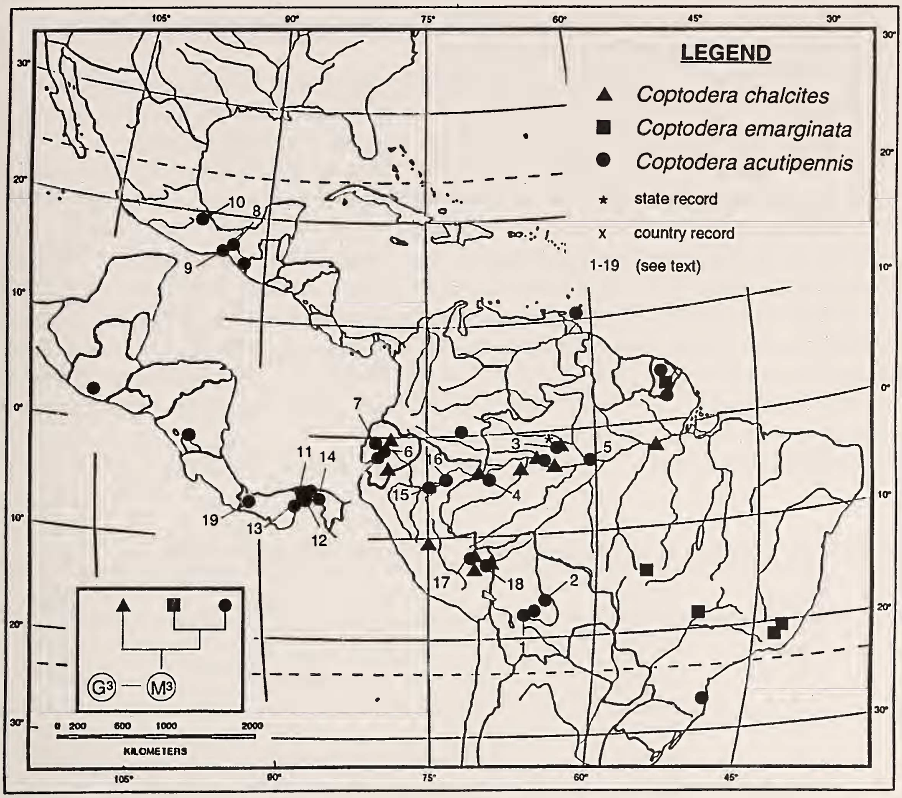


FIGURE 31. Line drawing of male genitalia of *C. acutipennis* (Buquet), morph J. Figs. A & B left lateral and dorsal aspects respectively. Scale bars = 1 mm. Legend: A, spine A; C, spine C.

them with the males when more than one type of male morph was found at a given locality. It is possible that some day molecular work will show these morphs to be distinct species.

Notes about habitat.-- Specimens were taken in Bolivia at an altitude of 430 m at fruitfalls and at rotting flood debris; in Ecuador at 100 to 280 m altitude at fruitfalls and in a Malaise-FIT trap; in México at 244 to 1010 m and at black light; in Panamá in litter along road at night, at light traps and at white and uv light; in Peru at 140 and 290 m altitude; at a figfall at night and at fermenting fruit of *Ficus* L.; and in Trinidad at 244 to 366 m altitude.

Geographical distribution (Map 15).-- The range of this species extends from the Southern Atlantic zone of southeastern South America north, from the Tropic of Capricorn, through the Amazon Basin to eastern México and the Gulf Versant, north of the Isthmus of Tehuantepec. In South America most of the range of *C. acutipennis* is cis-Andean, but one locality in Ecuador where specimens had been collected, is trans-Andean.



MAP 15. Geographical distribution of *Coptodera chalcites* Bates, *C. emarginata* Dejean and *C. acutipennis* (Buquet). Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for *C. emarginata* above, the adelphotaxon of *C. acutipennis*.

Material examined.-- We examined 93 specimens, including types, and saw non-type material from the following designated localities on Map 15 (letters and numbers following the coden indicate morph designation and number of males dissected respectively):

BOLIVIA Cochabamba. Region Chaparé (ZSMM); Villa Tunari (Loc. 1: UASM, H-1, J-1, M-1, N-2); **Sara**. (Loc. 2: MNHB, J-1). Collections in October and May.

BRAZIL Amazons (Loc. 3: BMNH, K-1), (MNHP); **Amazonas**. Benjamin Constant (Loc. 4: MZSP, K-1); Ega (MNHP); Manaus (Loc. 5: USNM, K-2); **Santa Catarina**. Hansa Humboldt (IZWP). Collection was made in September.

COLOMBIA Columb. Or. (MNHP).

COSTA RICA Puntarenas. 6 km s Sta. Elena (JEWC). Collection in June.

ECUADOR Napo Pastaza. Campana Cocha, e Puerto Misahuali (UASM); Limoncocha (Loc. 6: UASM, I-1); **Pichincha**. Rio Palenque Res. Sta., 47 km s Santo Domingo (Loc. 7: UASM, E-1)(CNC). Collections made in April to July.

FRENCH GUIANA Gourdonville (MNHP).
GUATEMALA Escuintla. Zapote (BMNH).
MÉXICO Chiapas. 1.4 km n Frontera Comalapa (UASM); 18.7 km n Ocozocuautla (Loc. 8: UASM, C-1); **Oaxaca**. 8 km e Tapanatepec, Rte. 190 (Loc. 9: UASM, B-2); **Veracruz**. Fortin de las Flores (Loc. 10: UCBC, A-1). Collections were made in June and July.
PANAMA Bocas del Toro. Almirante (USNM); Miramar 09°00'N 82°15'W (label reads Chiriqui province, which is incorrect if the latitude and longitude are correct) (Loc. 19: USNM, D-1); **Canal Zone**. Barro Colorado Is. (Loc. 11: USNM, C-1, D-2)(MCZ); Coco Solo Hosp. (Loc. 12: USNM, D-1); **Panamá**. Cerro Azul road nr Las Nubes (CAS); Cerro Campana (USNM); Cerro Campana, nr Chica (Loc. 13: UASM, C-1); dist. Chepo, Altos de Maje (Loc. 14: USNM, D-1); Ft. Gulick Rd. (USNM). Collections were made in March to May, July, September and November.
PERU Loreto. Cocha Shinguito (Loc. 15: UASM, F-4, J-1); Iquitos (Loc. 16: USNM, K-1); **Madre de Dios**. Pakitza, 12°07'S 70°58' (Loc. 17: USNM, L-1); Rio Tambopata Res. 30 km (air) sw Pto. Maldonado (Loc. 18: BMNH, G-1, J-9; CAS, G-1). Collections were made in August, November and February to April.
TRINIDAD Arima Valley (AMNH). Collection was made in November.

TABLE IX. Variation in Hw/Pw among adults of *Coptodera acutipennis* Buquet.

Morph	Country	N	Range	Mean
A[1]	México	1	0.77	0.77
B	México	2	0.76-0.77	0.77
C	México	2	0.72	0.72
D	Panamá	3	0.74-0.76	0.75
E	Ecuador	1	0.73	0.73
F	Peru	4	0.76-0.78	0.77
G	Peru	2	0.77-0.80	0.79
H	Bolivia	1	0.77	0.77
I	Ecuador	1	0.80	0.80
J	Bolivia	2	0.76-0.79	0.78
J	Peru[2]	9	0.75-0.80	0.78
J	Peru[3]	1	0.80	0.80
K	Brazil	4	0.72-0.760	0.75
K	Peru	1	0.76	0.76
L	Peru	1	0.78	0.78
M	Bolivia	1	0.82	0.82
N	Bolivia	2	0.78	0.78
-[4]	Panamá	2	0.72-0.75	0.74
-[5]	Peru	6	0.78-0.83	0.80
-	Bolivia	7	0.76-0.83	0.80
-	Panamá	8	0.73-0.79	0.75
-	México	3	0.75-0.80	0.78

[1] - alphabetical designations for males as described in text
[2] - state of Madre de Dios
[3] - state of Loreto
[4] - teneral males not dissected
[5] - sample of females from different countries (not all specimens included)

TABLE X. Variation in Pw/Pl among adults of *Coptodera acutipennis* Buquet.

Morph	Country	N	Range	Mean
A[1]	México	1	1.58	1.58
B	México	2	1.58-1.70	1.64
C	México	2	1.61	1.61
D	Panamá	3	1.62-1.71	1.65
E	Ecuador	1	1.68	1.68
F	Peru	4	1.52-1.55	1.54
G	Peru	2	1.53-1.56	1.55
H	Bolivia	1	1.48	1.48
I	Ecuador	1	1.50	1.50
J	Bolivia	2	1.55	1.55
J	Peru[2]	9	1.50-1.67	1.60
J	Peru[3]	1	1.50	1.50
K	Brazil	4	1.64-1.71	1.66
K	Peru	1	1.61	1.61
L	Peru	1	1.59	1.59
M	Bolivia	1	1.56	1.56
N	Bolivia	2	1.52-1.60	1.56
-[4]	Panamá	2	1.60-1.67	1.64
-[5]	Peru	6	1.53-1.67	1.60
-	Bolivia	7	1.52-1.62	1.57
-	Panamá	8	1.55-1.67	1.62
-	México	3	1.59-1.64	1.60

[1] - alphabetical designations for males as described in text
[2] - state of Madre de Dios
[3] - state of Loreto
[4] - teneral males not dissected
[5] - sample of females from different countries (not all specimens included)

Coptodera picea Group

This group has a single species which is characterized by finely setose labrum and clypeus, a shallowly emarginate anterior margin of labrum, which is wider than long, four discal setigerous punctures on each elytron, elytra unicolorous, reduced upper spur on inner surface of fore-tibia, and mid-tibia of male with notch on ventral surface near apex. See Table I for features of mandibles. Male genitalia with median lobe anopic; membranous portion medium-long; internal sac with macrospines (Figs. 32A-32B). Ovipositor with ensiform setae of stylomere 2 on dorsal margin (cf. Fig. 12I); nematiform setae present. The geographical range of this group is the most extensive, from cis-Andean South America, south of the Tropic of Capricorn north through Middle America to the Gulf Versant of México, south of the Tropic of Cancer, and to the tip of Florida.

Chorological affinities.-- The range of the *C. picea* group overlaps the southern part (South and Middle America) of the range of its adelphotaxon, the *C. aerata* group (Maps 16-20).

Phylogenetic relationships (Fig. 35).-- On the basis of shared apotypic features, reduced upper fore-tibial spur and anopic median lobe, this group is the adelphotaxon of the *C. aerata* group.

Coptodera picea Dejean
Figs. 4A-4F, 6C, 6G, 9C-9a, 32A & 32B; Map 16

Coptodera picea Dejean 1826: 458. Type material: LECTOTYPE (here selected) male, labelled: picea in Brazilia (Dejean's handwriting on green paper); Mannheim (Dejean's handwriting on green paper); Ex Musaeo Chaudoir (red print); TYPE (red paper); picea Dejean Brésil Coll. Dejean (Chaudoir Collection box label); LECTOTYPE ♂ Coptodera picea By Erwin '76; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Brazil.-- Chaudoir 1869: 178.

Coptodera velox Gory1833: 195. Type material: HOLOTYPE male, labelled: velox Cayenne (Dejean's handwriting on green paper); Lacordaire (Dejean's handwriting on green paper); velox Dej. TYPE (red paper); Ex Musaeo Chaudoir (red print); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Cayenne, French Guiana.-- Chaudoir 1869: 178.

Lebia rufula Buquet 1834: 680. Type material: HOLOTYPE male, labelled: Lebia rufula Buquet (handwritten); Ex Musaeo Chaudoir (red print); rufula Buq TYPE (red paper); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Cayenne, French Guiana.

Coptodera rufula: Chaudoir 1869: 178.

Coptodera unicolor Chevrolat 1834: No. [40]. NEW SYNONYMY. Type material: lectotype (here selected), female, labelled: Coptodera unicolor Chevr. Mexique; Chevrolat Carabidae Fr. V. d. Poll. Pres. 1909, E.B. Poulton; LECTOTYPE Coptodera unicolor Chev. By Erwin '76; TYPE Col: 126 Coptodera unicolor Chevr. HOPE DEPT. OXFORD [HECO]. Type area: México.

Coptodera obscura Laporte 1834: 51. Type material: not seen. Type locality: Orizaba, Veracruz, México.-- Chaudoir 1869: 178.

Notes about synonymy.-- The type specimen of *Coptodera unicolor* Chevrolat has the diagnostic character states of *C. picea* and we believe them to be conspecific. Based on examination of type material, we confirm the synonymy indicated by Chaudoir (1869: 178). We accept Chaudoir's synonymy of *C. obscura*.

Description.-- Character states of the *C. picea* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head, pronotum and elytra brunneous to nearly rufo-piceous; appendages, antennae, and mouthparts paler; lateral margin of elytron paler or not. Ventral surface rufo-brunneous to dark brunneous; epipleuron pale medially.

Mouthparts. Mandibles as in Figs. 4A-4F; labium as in Figs. 6C & 6G.

Elytra. Interneurs impunctate.

Legs. Fore-tibia as in Figs. 9C-9D; tarsal claws as in Fig. 9E.

Male genitalia. As in Figs. 32A-32B, median lobe with apical portion of medium length with ventral hook, hardly tapered before apex, in dorsal aspect trianguloid, slender; apex pointed in both lateral and dorsal aspects. Internal sac with spine A small; spine group B with two large spines; and spine group C absent.

Notes about variation.-- One female in a series of 15 specimens from Surinam has adhesive vestiture on tarsomeres 1 to 3 of the left front leg. The tarsomeres of the right front leg and the midtibia are unmodified.

Notes about habitat.-- Specimens were taken in the following countries at these altitudes: Bolivia, 500 m.; México, 30-880 m.; Peru, 290-840 m.; and Venezuela, 1370 m. Specimens were taken at u-v light traps in Belize and Honduras; from a Primavera log (*Cybistax* Mart. exx.

Meissn.) from Guatemala; from a light fixture in Honduras; at mercury vapor and u-v light and in bromeliads and on logs in México; by fogging the canopy with insecticide, at white light and on trails at night in Peru; by beating dead leaves in a cleared area in Trinidad; and at light in Venezuela. The Florida specimen was taken by beating dead (fire-killed) palmetto fronds in a burned pine scrub habitat.

Geographical distribution (Map 16).-- This species ranges from the Southern Atlantic zone northward through Amazonian Brazil and cis-Andean parts of South America to México north of the Isthmus of Tehuantepec, to Cuba in the West Indies, and to southern Florida.

Chorological affinities and phylogenetic relationships (Fig. 36).-- For details, see these topics for *C. picea* group above.

Material examined.-- A total of 309 specimens, including types were examined. Non-type material was seen from the following localities:

BELIZE Cayo. Augustine (CMNH); Western Hwy. Mi 66 (FSCA). Not located "M-tee dist." (MCZ). Collections in March, May, and July.

BOLIVIA (BMNH); **Beni**. 2 km n Guayaramerin (HNHM); Rurrenabaque, Rio Beni (USNM); **Sara**. Santa Cruz Dept. (MNHB). Collections in October and April.

BRAZIL (FMNH)(HNHM)(ZSMM); Amazon (MCZ); **Algoas**. São Miguel dos Campos (CMNH); **Amazonas**. Maturaca, alto Rio Cauaburi (MZSP); **Bahia**. (BMNH); **Espirito Santo**. Espirito Santo (BMNH); **Mato Grosso**. Chapada (=Chapada dos Guimaraes) (AMNH)(CMNH); **Minas Gerais**. Aguas Vermelhas (CMNH); **Para**. (BMNH); Monte Alegre (CMNH); **Rondônia**. Porto Velho, Rio Madeira (USNM); Rio Madeira, Madeira-Mamore R.R. Co. Camp 41 (USNM); **Santa Catarina**. Nova Teutonia (UASM); **São Paulo**. São Paulo (IZWP). Collections in October, December, January, and April.

BRITISH GUIANA Essequibo. Mataruki, Upper Essequibo (MCZ). Collection in December.

COLOMBIA (BMNH).

CUBA Camaguay. Camaguay (MCZ). Collection in September.

GUATEMALA Alto Verapaz. Cacao Trece Aguas (USNM); Chacoj (BMNH); Chiacaman (BMNH); Panzos (BMNH); San Cristobal Quixal (HFRE); 30 km nw San Cristobal (JEWC); **Izabal**. Cayuga (USNM); Yzabal (BMNH); **Petén**. Tikal (MZUM). One specimen ex. Guat. (USNM). Collections in April and May.

GUAYANA (MCZ).

HONDURAS (BMNH); **Atlandia**. Lancetilla, United Fruit Co. (FSCA); **Colón**. 3 mi sw Sonaguera (FSCA); **Guaimas**. Tela (MZUM). Collections in May, June, and August.

MÉXICO (BMNH)(IZWP)(MCZ); **Chiapas**. 6.3 & 7.4 km n Ocozocuautla (UASM); 16 km n Ocozocuautla (CNC); Hwy 199, 10 km s Palenque, San Manuel Rd. (LSUC); 18.3 km s Solosuchiapa, Rte. 195 (UASM); Tapachula (BMNH); 21.6 km w Tuxtla Gutierrez, Rte. 190 (UASM); **Quintana Roo**. 24 km n Carrillo Puerto (UASM); 17 km nw Felipe Carrillo Puerto (RHTC); 18-24 km n San Felipe, Carr. Pte. (JEWC); **San Luis Potosí**. Tamazunchale, Quinta Chilla (CAS); **Oaxaca**. Oaxaca (BMNH); **Tabasco**. La Chontalpa (USNM); **Veracruz**. Cerro de Plumas (="Cerro de Palmas") (AMNH)(BMNH)(MCZ); Cordova (BMNH); Cotaxtla Exp. Sta., Cotaxtla (UCBC); 15.3 km e El Tropico (UASM); Lake Catemaco (CNC); Motzorongo Sta. (MNHB); Playa Vicente (BMNH); 11.3 km n Santiago Tuxtla (UCBC); Sontecomapan (UASM); 4 km w Sontecomapan (UASM); Tuxtla (BMNH); **Yucatan**. 22 km ene Piste (RHTC). Collections in February to August and December.

NICARAGUA (BMNH); **Chontales**. (BMNH)(MCZ).

PANAMA Canal Zone. Barro Colorado Is. (USNM); Gatun (USNM); **Chiriquí**. Bugaba (AMNH)(BMNH)(MCZ)(USNM); V. de Chiriqui (BMNH)(MCZ)(USNM); Potrerillos (MCZ);

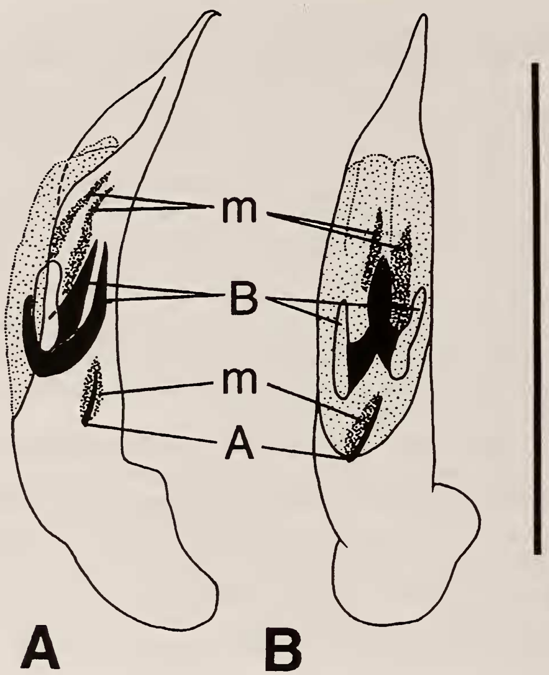
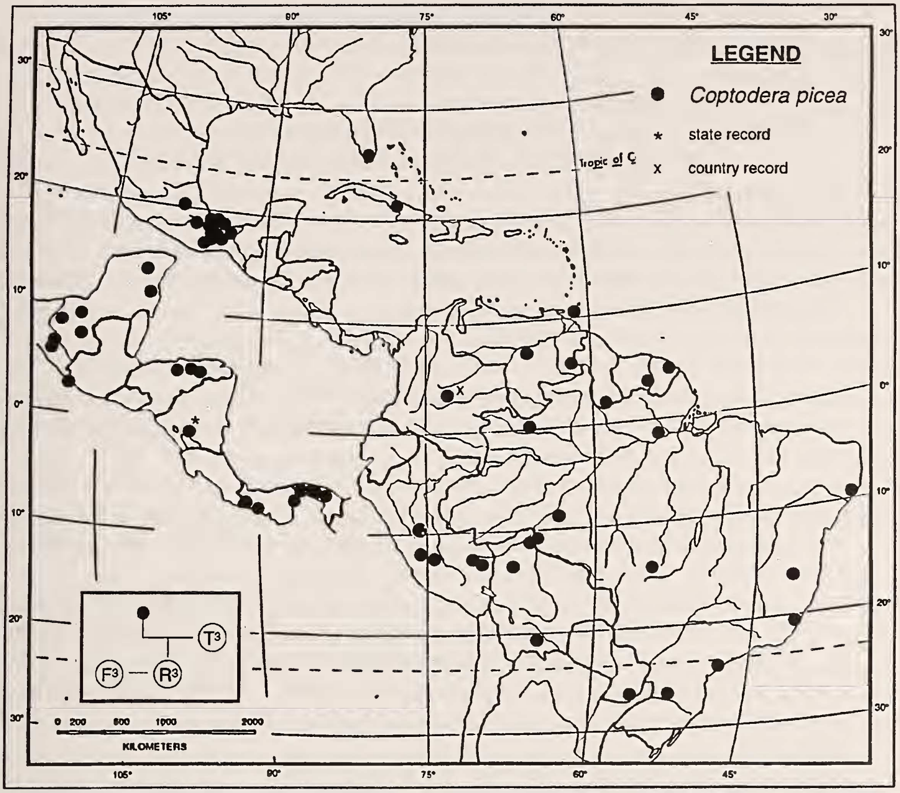


FIGURE 32. Line drawing of male genitalia of *C. picea* Dejean. Figs. A & B left lateral and dorsal aspects respectively. Scale bars = 1 mm. Legend: A, spine A; B, spine B; m, microtrichial field.

Darien. Santa Fe (OSUC); **Colon**. Sta. Rita Ridge (USNM); **Panamá**. Cabima (USNM); Cerro Campana (USNM); 11.3 mi sw Chepo (USNM); 80 km e Chepo (USNM); 11-15 km n El Llano (RHTC). Collections in April to July.
PARAGUAY Itapúa. Hohenau (IZWP); Hohenau, Alto Parana (UASM).
PERU Huanuco. Tingo Maria (AMNH); **Junín**. Chanchamayo (MNHB); Sani Beni, 8 km e Satipo (SEMC); Satipo (MCZ)(USNM); **Madre de Dios**. Pakitza, 11°55'48"S 71°35'18"W (USNM); Pakitza, 12°07'S 70°58'W (USNM); Rio Tambopata Reserve, 30 km (air) se of Puerto Maldonado 12°50'S 69°20'W (DHK)(USNM). Collections in July, and September to November.
SURINAM Marowijne. Anapaike, Rio Lawa (MZSP). Collections in November.
TRINIDAD Valencia (MCZ). Collection in May.
U.S.A. Florida. Collier Co. hwy. 41, 2.4 km. s. jct. hwy. 951 (RHTC). Collection in April.
VENEZUELA Bolivar. La Gran Sabana, Chivaton Hotel, on rd. to Kavanayen (IVIE); Suapure, Caura River (CUIC). Collections in April and June.



MAP 16. Geographical distribution of *Coptodera picea* Dejean. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

Coptodera aerata Group

This group includes five species, characterized by a ventral sensory pit on antennomeres 5-11, finely setose labrum and clypeus, a deeply emarginate anterior margin of labrum, which is wider than long, three or four discal setigerous punctures (indicated in the species description) on each elytron, elytra unicolorous to bicolored (not a variegated color pattern), markedly reduced upper spur on the inner surface of the fore-tibia, and male mid-tibia with notch on ventral surface near apex. See Table I for features of mandibles. Male genitalia with median lobe anopic, membranous portion various in length; internal sac with macrospines (Figs. 34A-34H). Ovipositor with stylomere 2 as in Figs. 12M-12P; ensiform setae on dorsal margin; nematiform setae present. The geographical range of this group extends from north eastern United States south through México and Central America into South America, both trans- and cis-Andean, to southeastern Brazil, in the Southern Atlantic zone (Maps 17-20).

Chorological affinities and phylogenetic relationships.-- See discussion for these topics under the appropriate headings for the *C. picea* group.

Coptodera nitidula (Buquet)
Figs. 1A, 1G, 4G-4L, 9F-9H, 33A-33C, 34A & 34B; Map 17

Lebia nitidula Buquet 1834: 677. Type material: HOLOTYPE male, labelled: Ex Musaeo Chaudoir (red print); nitidula (Lebia) Buquet Brésil Sahlberg jun (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Brazil.-- Chaudoir 1869: 185.-- Bates 1870: XVI.

Coptodera nitidula: Chaudoir, 1869: 185.

Lebia triangularis Buquet 1834: 678. NEW SYNONYMY. Type material: HOLOTYPE male, labelled: Ex Musaeo Chaudoir (red print); triangularis Buquet (Lebia) Amazone Bates (original box label); Paris Museum ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Cayenne, French Guiana.

Coptodera triangularis: Chaudoir 1869: 185.

Coptodera luculenta Erichson 1847: 69. Type material: HOLOTYPE male, labelled: luculenta Erichs; Ex Musaeo Chaudoir (red print); Paris Museum ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Peru.-- Chaudoir 1869: 185.

Coptodera debilis Bates 1869: 76. Type material: LECTOTYPE (here selected) female, labelled: LECTO (red paper); TYPE (red paper); S. Paulo Amaz (Bates' handwriting); debilis Bates (Bates' handwriting); nitidula Buq sec Chaud (Bates' handwriting); ex Musaeo H.W. Bates 1892; LECTOTYPE Coptodera debilis Bates det. George E. Ball '87; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: S. Paulo, Amazonas, Brazil.-- Bates 1870: XVI.

Coptodera nubiculosa Chaudoir 1869: 186. NEW SYNONYMY. Type material: LECTOTYPE male (here selected) labelled: Ex Musaeo Chaudoir (red print); TYPE (red paper); nubiculosa Chaud Paramaribo Dohrn (original box label); Paris Museum ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Paramaribo, Surinam.-- Jeannel 1949: 926.-- Reichardt 1977: 446.

Coptodera flavodisca Chaudoir 1869: 187. NEW SYNONYMY. Type material: HOLOTYPE female, labelled: (green rectangle); Ex Musaeo Chaudoir (red print); HOLO (red paper); TYPE (red paper); HOLOTYPE Coptodera flavodisca Chaud det. George E. Ball '72; flavodisca Chaud Amazons Bates (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega, Amazonas, Brazil.

Coptodera flavodisca immaculipennis Bates 1883: 182. NEW SYNONYMY. Type material: LECTOTYPE (here selected), labelled: S. Geronimo Guatemala Champion; B.C.A. Col. I.1 Coptodera flavodisca, Chaud; Copt. flavodisca v. immaculipennis (Bates' handwriting); LECTOTYPE Coptodera immaculipennis Bts. By Erwin '76 [BMNH]. Type locality: San Jerónimo, Baja Verapaz, Guatemala.

Notes about type material.-- In the MNHP is a female specimen labelled as follows: Ex Musaeo Chaudoir (red print); Museum Paris ex Coll R. Oberthür (light green paper); rufodiscus Chaud Neuv. Grenada Lindig (original box label). It appears that perhaps Chaudoir intended to use "*rufodiscus*" for this species, but did not publish this name, instead publishing the name "*flavodiscus*".

Notes about synonymy.-- Adults of all of the above named forms show intermediate color patterns of the elytra, ranging from unicolorous, small pale area on darker background, darker markings on pale background (Fig. 33C), markedly pale disc (Fig. 33A) to dark diagonal markings on pale background (Fig. 33B). All of these specimens have identical male genitalia throughout the known range, and we believe them to be conspecific. The oldest available name is *C. nitidula* (Buquet), and all other names are junior synonyms.

Notes about classification.-- Jeannel (1949: 926), under the specific epithet *nubiculosa*, assigned this species to the otherwise African genus *Haplocrepis*. However, the similarities in genitalic structure among the Afrotropical and Neotropical species are considered convergent-apotypic, or symplesiotypic. As Reichardt (1977: 446) pointed out, Ball (1975) did not consider *Haplocrepis* in his ostensibly complete treatment of the New World pericaline genera.

Recognition.-- Within the *C. aerata* group, this species has the longest sensory pits on the ventral surface of antennomeres 5-11 (Fig. 1A).

Description.-- Character states of the *C. aerata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum testaceous to brunneous; elytra unicolorous, with faint greenish lustre, rufo brunneous to brunneous, or bicolored, brunneous to piceous with testaceous to brunneo-testaceous markings, lateral margin paler, testaceous to rufo-testaceous; mouthparts, antennae, and legs testaceous to rufo-testaceous. Ventral surface testaceous to dark brunneous.

Mouthparts. Labrum as in Fig. 1G; mandibles as in Figs. 4G-4L.

Elytra (Figs. 33A-33C). Interneurs impunctate to finely punctulate.

Legs. Fore-tibia as in Figs. 9F-9G; tarsal claws as in Fig. 9H.

Male genitalia. As in Figs. 34A-34B, median lobe with membranous portion medium-short to medium. Apical portion medium-short to medium, flattened, in lateral aspect trianguloid, slender, tapered to apex, in dorsal aspect trianguloid, broad; apex in lateral and dorsal aspect pointed. Internal sac spine A large; spine group B two medium to large spines; spine group C one spine of medium size.

Notes about variation.-- This species has several elytral color patterns, three of them are shown in Figs. 33A-33C.

Notes about habitat.-- Specimens were taken in the following countries at these altitudes: Bolivia, 400 m.; Brazil, 100 m.; Costa Rica, 600-1100 m.; Ecuador, 250-305 m.; Guatemala, 914-1706 m.; México, 975-1548 m.; Panamá, 243-1524 m.; Peru, 200-2300 m.; United States, 1158-1737 m. Specimens were taken in an inundation forest in Bolivia; under bark and in fibres of cut wood in Brazil; under bark in Costa Rica (and on dry bark), México and Panamá; at uv light in Costa Rica and México; in bromeliads in México; at lights in Panamá and United States; in Peru, at molasses traps, under bark and under rotting log in sandy soil; in Surinam, on a fresh cut stump of *Simarouba* Aubl.; and in United States, at mercury vapor lights and on a dead oak at night.

Geographical distribution (Map 17).-- This species ranges from Arizona in southwestern United States south through México on Pacific and Gulf Versants, through Middle America to the Chacó area of trans-Andean Ecuador, and to the Southern Atlantic zone of eastern Brazil.

Chorological affinities.-- The geographical range of this species overlaps broadly the ranges of its adelphotaxon *C. brunnea* + *C. waytkowskii*.

Phylogenetic relationships (Fig. 36).-- *Coptodera nitidula* is postulated to be the adelphotaxon of *C. brunnea*.

Material examined.-- A total of 264 specimens, including types, were examined. Non-type material was seen from the following localities:

ARGENTINA Misiones. Gob. Misiones (MNHB).

BOLIVIA Beni. Rurrenebaque (CAS); 40 km e San Borja, Estacion Biologica Beni, Palm Camp at Rio Curiraba (USNM); **Cochabamba**. (MNHP); Region Chaparé (ZSMM); **La Paz**. Tumupasa (USNM); **Santa Cruz**. Buena Vista (FSCA). Not located: R. Japacani (CMNH). Collections were made in September, December and January.

BRAZIL Amazon (BMNH); Amazons (BMNH); S. Brazil (MCZ); **Amapa**. Pôrto Santana (USNM); **Amazonas**. Ega (MNHP); Manaus, 1 km w Taruma Falls (CMNH); AM 010, km. 26, Reserva Ducke (USNM); São Paulo de Olivença (MNHP); **Bahia**. (MNHP); **Goiás**. Jatahy (MNHP); **Mato Grosso**. Xingu (MZSP); **Para**. (BMNH)(MNHP); Belem (ZSMM); Bragance (MNHP); **Parana**. Londrina (MCZ); Rondon (MCZ); **Rondônia**. Rio Madeira (USNM); Rio Madeira, Madeira-Mamore R.R. Camp 41 (USNM). **Santa Catarina**. (MNHP); Cauna (AMNH); Corupa (AMNH); Hansa Humboldt (BMNH)(MCZ); Nova Teutonia (BMNH)(MCZ); **São Paulo**. (MNHP); Barueri (MZSP). Collections in September to January, March to May, and July.

COLOMBIA (MNHP).

COSTA RICA Alajuela. Peñas Blancas (UASM); Rio Sarapiqui, 6 air km s San Miguel (UCBC); **Cartago**. 3 km se Turrialba (UCBC); Turrialba (UASM); **Guanacaste**. Carillo (USNM); **Limón**. Hamburg farm (USNM); Hamburg farm, Reventazon (IZWP); Valle de la Estrella Pandora (UASM); **Puntarenas**. 14 km s San Vito de Java (USNM); **San José**. San Carlos (USNM). Collections in January to July, September, and October.

ECUADOR Bolívar. Chimbo (BMNH); **Pichincha**. Rio Palenque (UASM); Rio Palenque, 47 km s St. Domingo (CNC)(UASM); Rio Palenque Station, 47 km s Sto. Domingo (CNC)(UASM); Tinlandia, 17 km e Santo Domingo de los Colorados (UASM). Collections in February, May and July.

GUATEMALA Alta Verapaz. Balheu (BMNH)(MNHP)(USNM); S. Geronimo (BMNH)(MNH) (USNM); Tamahú (BMNH)(MNH); **Chimaltenango**. Mun. Yepocapa (FMNH); **Escuintla**. Zapote (BMNH); **Sacatepéquez**. Capetillo (BMNH); **San Marcos**. El Tumbador (BMNH); El Zumbador (MNHP). Collections in May.

GUYANA Essequibo. Essequibo R., Maraballi Creek (IZWP). Collections in August.

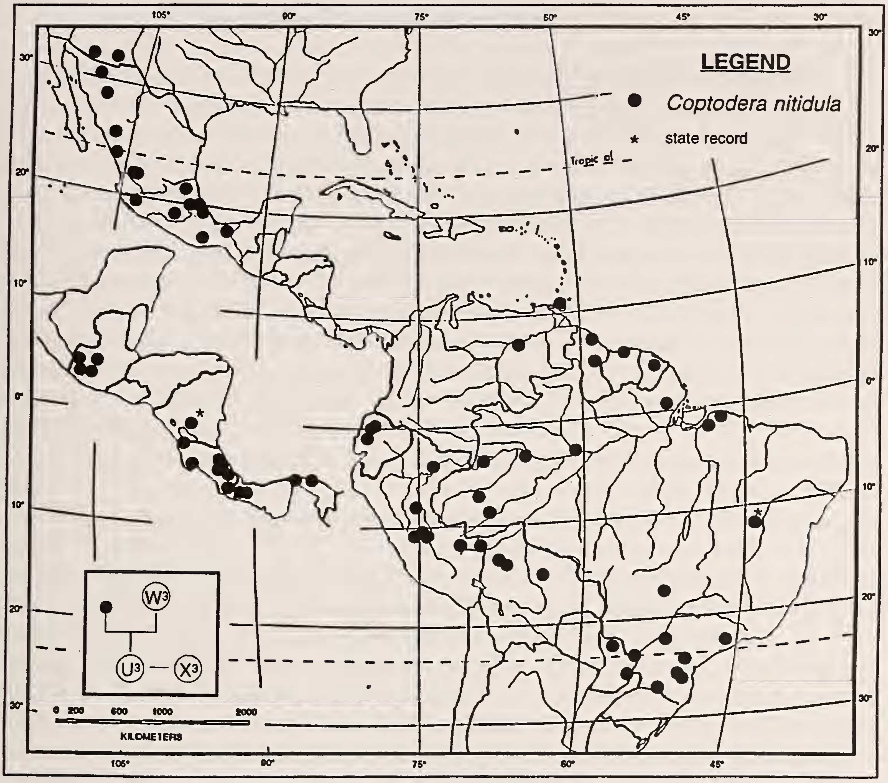
MÉXICO (BMNH)(IZWP); **Chiapas**. 18.7 km n Ocozocuautla (UASM); **Colima** se slope of Mt. Colima (CAS); **Morelos**. 8.7 km e Cuernavaca (UASM); 14.6 km e Cuernavaca, Canyon de Lobos (UASM); **Nayarit**. Arroyo Santiago, nr Jesus Maria (UCBC); La Mesa de Nayar (CAS)(UCBC); **Oaxaca**. 24.8 km s Juchatengo (UASM); **Puebla**. 14.5 km se Izucar Matamoros (CNC); 24.1 km e Teziutlan (CNC); **Queretaro**. 8.3 and 26.5 km w San Luis Potosí Queretaro border, Hwy. 120 (SEMC); **Sinaloa**. 12.9 km w El Palmito (UASM); **Sonora**. 14.5 km s Cananea (FSCA); Rancho Aguajia, 16 km nw Yecora (UASM); 6.4 km ne Yecora on road to Maycoba (UASM); **Veracruz**. Cerro de Plumas (BMNH)(MNHP); Jalapa (AMNH). Collections in March, May to September, November, and December.

NICARAGUA Chontales. (BMNH)(MCZ).

PANAMA Canal Zone. Barro Colorado, Gatun Lake (USNM); Barro Colorado Is. (USNM); 5-8 mi nw Gamboa, Pipeline Road (USNM); **Chiriqui**. Bugaba (BMNH); Miramar 09°00'N 82°15'W (USNM); Ojo de Agua, 4 km n Santa Clara (UASM); V. de Chiriqui (BMNH)(MNHP); **Panamá**. Altos de Maje, dist. Chepo (HPST). Not located "Potreriles" (CAS), which may be a misspelling of Potrerillos. Collections in May to September.

PARAGUAY Alto Parana. Puerto P. Stroessner (HNHM); **Concepción**. Horqueta (MCZ); vic. Horqueta (MCZ); **Itapúa**. Hohenau (UASM). Collection in October.

PERU east Peru (MNHP); **Huánuco**. Bella Durmiente, nr Tingo Maria (UASM); Monzon Valley, Tingo Maria (CAS); Tingo Maria (AMNH)(MCZ). **Junín**. between San Ramon de Pangoa and Boca de Kiatari, 40-55 km se Satipo (AMNH); Sani Beni, 8 km e Satipo (SEMC); Satipo (IZWP)



MAP 17. Geographical distribution of *Coptodera nitidula* (Buquet). Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

(USNM); Viena (SEMC); **Loreto**. Amazon Camp, Rio Momóm, near Iquitos (CAS); **Madre de Dios**. Pakitza, 12°07'S 70°58'W (USNM); 15 km ne Puerto Maldonado (SEMC). Collections were made in April, June to August and October to December.

SURINAM Bakhuis Gebergte (UASM); Brokopondo, Baboenhol Ranch (BMNH). Collections in January, March, and August.

TRINIDAD Arima, Verdant Valle (MCZ).

U.S.A. Arizona. Santa Cruz Co. Coronado Nat. For., Walker Canyon on FSR 221, 1.4 km s Hwy 289 (UASM); Pajarito Mts., Pena Blanca (FSCA); Pajarito Mts., Peña Blanca Can. (SMC); Pajarito Mts., Walker Cn. (SMC); Peña Blanca (UASM); **New Mexico**. Hidalgo Co. Guadalupe Canyon (CAS). Collections in July to September.

VENEZUELA Bolivar. Saupure, Caura River (CUIC). Collections in March to May.

Coptodera brunnea, new species
Frontispiece; Figs. 1B, 34C & 34D; Map 18

Type material.-- HOLOTYPE male, labelled: AZ: COCHISE CO. Guadalupe Can. vii-15-78 1300M at lite McCleve [USNM]. ALLOTYPE female, labelled: same as holotype [USNM]. 149 additional PARATYPES, sex and label data as follows: 3 females: same as holotype [SMC]. 1 male and 1 female: AZ:COCH.CO. Les- lie Cn vii-11-76 ex bait trap Scott McCleve [SMC]. 1 male: AZ: COCHISE CO. Chiricahua Mts. Horseshoe Can. vi-27-78 1511M at lite McCleve. 2 females: AZ:COCHISE CO. Guadalupe Can. vi-30-77 at lite S.McCleve [SMC]. 1 female: AZ:COCHISE CO. Douglas 1241m VI-18-72 at lite S.McCleve [SMC]. 1 female: Peloncillo Mtns, 33miE Douglas, AZ 7-17-1973 at light S.McCleve [SMC]. 1 male: Chiricahua M. VII-16-59 Ar.; D.J. & J.N. Knull Collrs. [OSUC]. 1 female: Chiricahua M. VIII-7-59:Ar.; D.J. & J.N. Knull Collrs. [OSUC]. 1 female: ARIZONA Chiricahua Mts elev. 4000 ft. Aug. 3 1969 [FSCA]. 1 female: U.S.A.,Ariz. Cochise Co. Chiricahua Mt. S. Fork Cn.; Lot No 824VII-13-1964 R.H. Arnett, Jr ER. VanTassell [FSCA]. 44 males and 36 females: AZ: Cochise Co. Huachuca Mtn. Ash Canyon Rd. (1/2 m. W Hwy 92) (5100') 2-5.VIII.89 Y.Bousquet [BMNH][CNC][MCZ][MNHP]. 1 female: Miller Canyon 5000' Huachuca Mountains Cochise Co., Ariz. 1 July 1974 E.R. Hoebeke [CUIC]. 1 female: Miller Canyon 5000' Huachuca Mountains Cochise Co., Ariz. 5 July 1974 E.R. Hoebeke [CUIC]. 1 female: AZ:Pima Co' Green Valley VIII-1973 Lonczy [CAS]. 1 male: MaderaCn. Pima Co. Arizona DrLenczy VI.1976; DAVIDSON COLLECTION Donated 1989; Coptodera unicolor Chev. [CMNH]. 1 female: MaderaCn. Pima Co. Arizona DrLenczy 7.1975; DAVIDSON COLLECTION Donated 1989; Coptodera unicolor Chev. [CMNH]. 1 male: ARIZ: Pima Co. Madera Cyn. 7. 1975 Dr. R. Lenczy [CMNH]. 1 male: ARIZ: Pima Co. Madera Cyn. VI. 1976 Dr. R. Lenczy [CMNH]. 1 female: Sta. Catalina Mts. II.26.1935 Ariz. Bryant, Lot 4 [CAS]. 1 male and 1 female: AZ:STA CRUZ CO. Pajarito Mts. Pena Blanca Can vii-2-80 1191m at lite McCleve [SMC]. 1 female: AZ:STA CRUZ CO. Pajarito Mts. Pena Blanca Cn vii-30-81 1191m at lite McCleve [SMC]. 1 male: Madera Canyon Sta. Rita Mts. Santa Cruz Co. ARIZ. 4860 ft.; Collected by J.D.Marshall June 23,1963 [CUIC]. 2 males: Arizona:Santa Rita Mts. Madera Cyn. July 3 1968 [AMNH][FSCA]. 1 female: ARIZONA Sant Rita Mts. Madera Cyn. 1 Aug 1970 K.Stephen call. [AMNH]. 1 male and 1 female: U.S.A.ARIZONA Sta.Rita Mts Madera Cn.VII.1968 leg.Dr.R. Lenczy [HNHM]. 1 female: Patagonia M. VIII-3-55.Ar.; D.J. & J.N. Knull Collrs. [OSUC]. 1 female: Arizona Peña Blanca VII.16.68 [AMNH]. 1 male: Arizona; Pajarito Mts. Pena Blanca July 13 1968 [FSCA]. 1 male: ARIZONA Pajarito Mts. Pena Blanca Cyn. 13 July 1970 K.Stephen coll. [FSCA]. 1 female: ARIZONA Pajarito Mts. Pena Blanca Cyn. 11 July 1970 K.Stephen coll. [FSCA]. 1 female: Arizona:Santa Rita Mts. Madera Cyn. July 24 1968 [FSCA]. 1 male: Ariz.Santa Cruz Co. Madera Canyon,5100' Bog Spring Cp.Grd. Santa Rita Mts. D. Davis,VII-10-26-64 [USNM]. 1 female: U.S.A.,Ariz. Santa CruzCo Pajarito Mts Pena Blanca Black light; Lot No.176 VII-26-1964 Evening J.Stibick [USNM]. 1 male: ARIZONA:St. Cruz Co. 3.2 Km S.Pena Blanca Lake.1250 m., VII-28-1989: R.S. Anderson & S.McCleve: UV light [TAMU]. 1 male: Santa Rita Mts. Ariz. 5 to 8000ft. July. F.H. Snow.; 10; H. C. FALL COLLECTION [MCZ]. 2 males: 6000ft Mt. Washington NogalesAriz. VII-20-1919; Van Dyke Collection [CAS]. 1 male: 6000ft Mt. Washington NogalesAriz. VII-19-1919; Van Dyke Collection [CAS]. 1 male and 2 females: USA AZ,SantaCruz Co. Coronado N.Forest Walker Cyn. on FSR 221.1.4km S. Hwy 289 11.VIII.89 Pollock; at black & Hg-vapor lights [UASM]. 3 females: Ariz. Santa Cruz Co. .5 mi. W Upper White Rock Cmgd., 27 July 1989 R. Turnbow [RHTC]. 1 female: NM: Chaves Co. Bottomless Lakes S.P., 7.VIII.89 Y.Bousquet [gypsum flats] [CNC]. 1 female: MEXICO. Chiapas 5km E.Ocozocaut la 820m. 4.VI.1990 H. & A. Howden;

at light [UASM]; 1 male: MEX. Chiapas,Parque Laguna Belgica 27-V-1987, D.A. Rider E. G. & T.J. Riley; collected at mercury vapor & blacklight [LSUC]; 1 male: MEX. Veracruz Rancho Clacotengo,ca.2-5km. n. Fortin de las Flores,1120m.,pasture in bromeliads 78B-32 December 21, 1978; MEXICAN EXP. 1978-1979 G.E.&K.E. Ball Collectors [UASM]. 1 male: Mexico, Rascón zw.SanLuisPotosi u.Tampico VIII.1911 C.A.Purpus S.V. [MNHB]. 1 female: Chiacaman, Vera Paz. Champion; B.C.A. Col. I.1 Coptodera unicolor, Chevr. [BMNH]. 1 female: BRITISH HONDURAS Cayo Dist. Augustine Pine Ridge Forest Station, u.v.light 3-VII-68. W.L.Hasse [FSCA]. 1 male: BRITISH HONDURAS Cayo Dist.Augustine Pine Ridge, u.v.light 4-VII-1968 W.L.Hasse [FSCA]. 1 male and 1 female: BR.HONDURAS Belize District WesternHwy Mi 15 08 Jun 1968 Light:UV, trap; Hasse,W.L. Collector [FSCA]. 1 male: HONDURAS., Dept.Comajagua, Rancho Chiquito Km.62,UV-light, 29 May 1964; F.S. Blanton, A.B. Broce, R.E. Woodruff, Collectors [FSCA]. 3 males and 2 females: BELIZE:Cayo District Mountain Pine Ridge, Hidden Valley. 650- 700m. 89-00W,17-00N; 24 May 1990 Norton S. Adams, Linwood C. Dow Pine-oak savanna [CMNH]. 3 males: BELIZE:Cayo District Mountain Pine Ridge, Hidden Valley. 650- 700m. 89-00W,17-00N; 22-29 May 1990 Norton S. Adams, Linwood C. Dow pine-oak savanna [CMNH].

Type locality.-- Guadalupe Canyon, Cochise County, state of Arizona, United States of America.

Derivation of specific epithet.-- From Medieval Latin *brunneous*, in allusion to the brown color of this species.

Recognition.-- This species is readily separated from the other species of the *C. aerata* group by a combination of the following three characters: brown color, antennomeres 3 and 4 darkened, and small sensory pits on the ventral surface of antennomeres 5-11 (Fig. 1B).

Description.-- Character states of the *C. aerata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head, pronotum and elytra rufo-brunneous to dark brunneous; lateral margin of elytron paler or not; antennae rufous, antennomeres 3 and 4 darkened (contrasting with antennomeres 2 and 5); mouthparts rufous to rufo-brunneous; appendages brunneous, femora paler basally. Ventral surface brunneous to dark brunneous; epipleuron paler medially.

Elytra. Interneurs impunctate.

Male genitalia. As in Figs. 34C-34D, median lobe with membranous portion short. Apical portion medium, flattened, in lateral aspect trianguloid, rather broad, in dorsal aspect trianguloid, broad; apex in lateral aspect narrowly rounded, in dorsal aspect broadly rounded. Internal sac spine A medium in size; spine group B absent; spine group C with three medium-small spines.

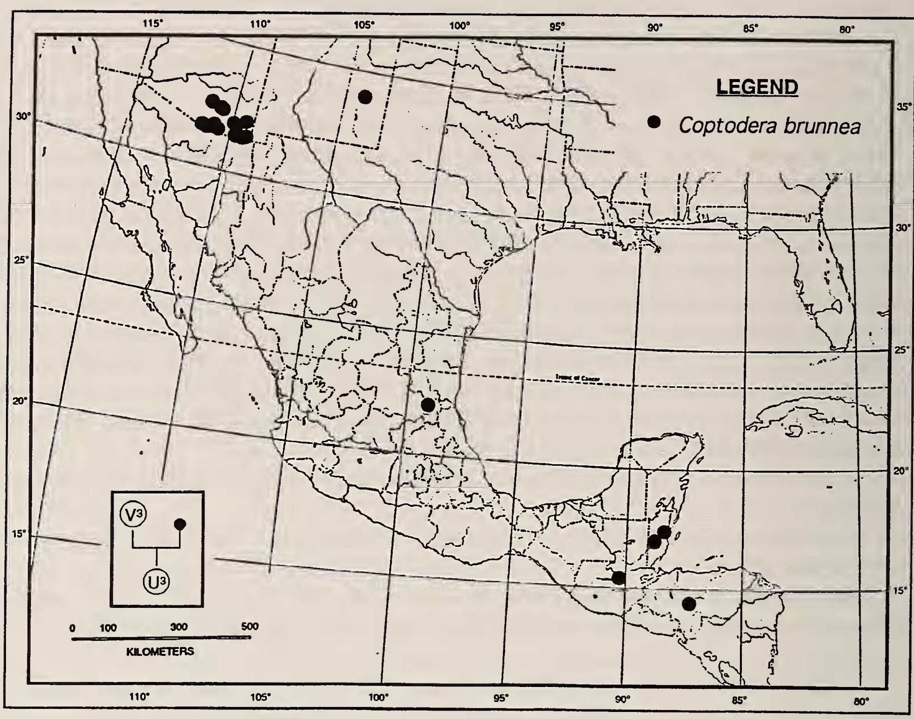
Notes about habitat.-- In Belize and Honduras specimens were taken at u-v light. In México, one specimen was taken at an altitude of 1120 m from bromeliads in a tree growing in a pasture; a second at mercury vapor and blacklight. In United States, specimens were taken at altitudes of 1191-1828 m; at blacklight; at mercury vapor lights; at light; and in bait traps.

Geographical distribution (Map 18).-- This species ranges from Nuclear Central America (Honduras and Belize) northward on the Gulf Versant of México to the southwestern United States.

Chorological affinities.-- The range of *C. brunnea* is overlapped completely by the range of its adelphotaxon, *C. nitidula* (Maps 17 and 18).

Phylogenetic relationships.-- See topic for *C. nitidula* above, the adelphotaxon of *C. brunnea*.

Material examined.-- Type material only; see above for details.



MAP 18. Geographical distribution of *Coptodera brunnea*, new species. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

Coptodera aerata Dejean
Figs. 1H, 6D, 6H, 12M-12P, 34E & 34F; Map 19

Coptodera aerata Dejean 1825: 277. Type material: LECTOTYPE (here selected) male, labelled: TYPE (red paper); aerata in Amer bor (Dejean's handwriting on green paper); Ex Musaeo Chaudoir (red print); LECTO- TYPE (disc with purple border); LECTOTYPE Coptodera aerata Dej. det. George E. Ball '72; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: United States.-- LeConte 1848: 196.-- Horn 1881: t. 8, f. 84.-- 1882: 131.-- Blatchley 1910: 149.-- Ball 1960: 158.

Coptodera viridipennis Gory 1833: 194. Type material: HOLOTYPE male, labelled: viridipennis LeConte Gory; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: United States (incorrectly given in the original description as Java).-- Chaudoir 1869: 179.

Coptodera viridipennis LeConte 1848: 196. Type material: LECTOTYPE (here selected) male, labelled: orange disc (south-eastern United States); var. viridipennis LeC. [MCZ]. Type locality: Alabama, United States.-- Horn 1882: 160.

Coptodera ruficornis Chaudoir 1869: 179. Type material: LECTOTYPE (here selected) female, labelled: LECTO (red paper); TYPE (red paper); ruficornis Chaud (handwritten); Louisiane Guex (handwritten); Ex Musaeo Chaudoir (red print); LECTOTYPE Coptodera ruficornis Chaud det. George E. Ball '87; Museum Paris ex Coll R. Oberthür (light green paper)[MNHP]. Type locality: Louisiana, United States.-- Horn 1882: 160.

Note about synonymy.-- We confirm the synonymy by Chaudoir and Horn, noted above, based on the study of type material.

Notes about type material.-- Chaudoir (1869: 179) listed *C. viridipennis* Gory as a junior synonym of *C. aerata* followed by a reference to LeConte's publication. Gory's collection of Carabidae was acquired by Chaudoir in 1852 (Basilewsky 1983: 465). In the MNHP there is a Chaudoir specimen bearing a label "viridipennis LeConte Gory". We believe that this specimen is Gory's type, and was labelled by Chaudoir indicating that *C. viridipennis* of both LeConte and Gory was the same species. Gory's material must have been incorrectly labelled as this species is known only from United States.

Notes about nomenclature.-- Although the name *Coptodera viridipennis* LeConte is a junior primary homonym of *C. viridipennis* Gory, according to the International Code of Zoological Nomenclature (Third Edition, Article 60), a replacement name is not required for *C. viridipennis* LeConte because this name is a junior subjective synonym.

Description.-- Character states of the *C. aerata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum brunneous to rufo-piceous with faint green lustre; elytra metallic green to blue-green, at times aeneous laterally; antennae, mouthparts and appendages brunneous. Ventral surface brunneous to dark brunneous.

Fixed setae. Disc of elytron with three setigerous punctures.

Mouthparts. Labrum as in Fig. 1H; labium as in Figs. 6D & 6H.

Elytra. Interneurs impunctate.

Male genitalia. As in Figs. 34E-34F, median lobe with membranous portion medium-short. Apical portion medium-long, in lateral aspect trianguloid, slender, tapered gradually toward apex, in dorsal aspect trianguloid but constricted preapically; apex in lateral aspect narrowly rounded, in dorsal aspect sub-truncate. Internal sac spine A small; spine group B with two small spines; spine group C with two small spines.

Ovipositor. Stylomere 2 as in Figs. 12M-12P.

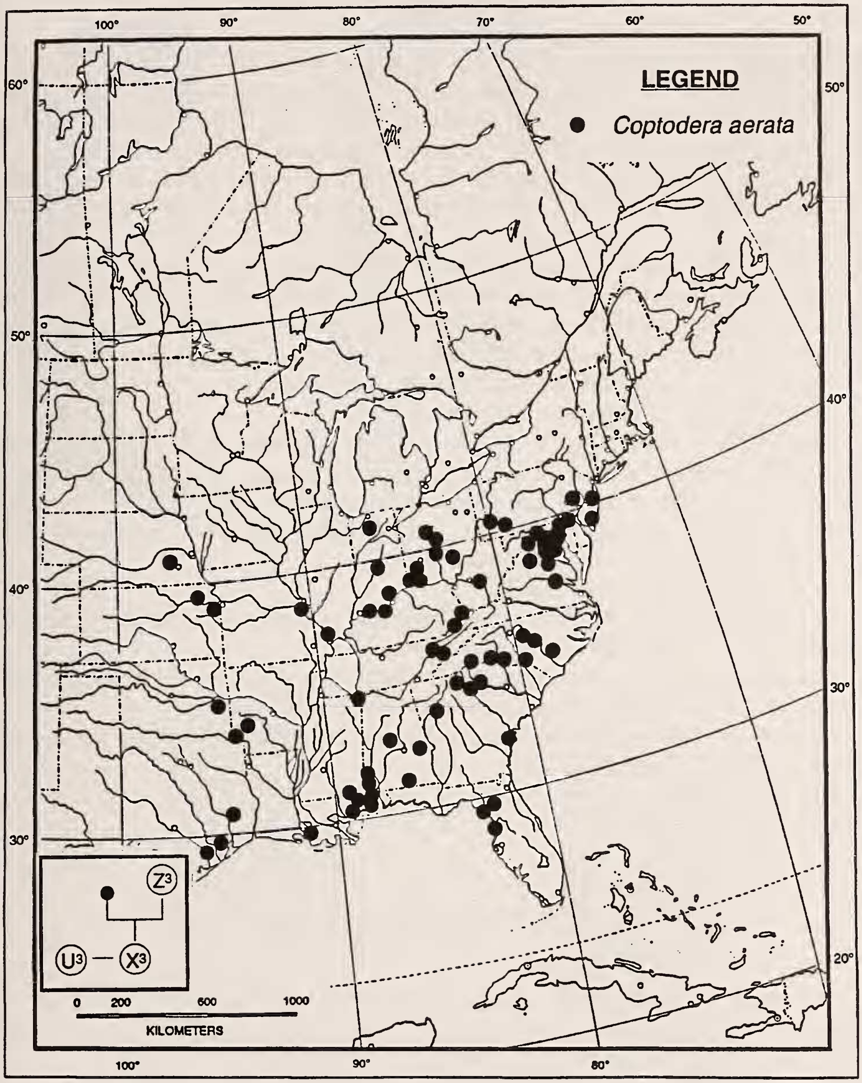
Notes about habitat.-- Specimens were taken at altitudes of 30-762 m. Specimens were taken at light, both white and uv; under bark; under cyprus and oak bark; on dead oak and beech; by sweeping oak; in garbage; in a light trap at a tobacco warehouse; and by beating in upland and lowland forest.

Geographical distribution (Map 19).-- This species is found in the United States only, and probably only in the forested areas of the east, and the gallery forests of the Mississippi drainage basin, in the west. We believe the Montana specimen is mislabelled and the Arizona specimen is probably mislabelled.

Chorological affinities.-- The range of *C. aerata* is separated widely from that of its adelphotaxon, *C. waytkowskii* (Maps 19 and 20). In fact, *C. aerata* is isolated geographically from all other known species of *Coptodera*.

Phylogenetic relationships (Fig. 36).-- Based on the derived feature of reduced spines in the internal sac (Figs. 34E & 34F; cf. Fig. 34G & 34H), this species and *C. waytkowskii* are postulated to be adelphotaxa.

Material examined.-- A total of 490 specimens, including types, were examined. Non-type material was seen from the following localities:
U.S.A. Alabama. Dale Co. Ft. Rucker Mil. Res. (RHTC); Jefferson Co. Birmingham (FMNH); Lee Co. Auburn (USNM); Mobile Co. 18.2 km e Citronelle (AMNH); Magazine Pt. (CAS); Mobile (MCZ); Mt. Vernon (CAS); **Arizona**. Santa Cruz Co. Peña Blanca (AMNH); **Arkansas**. Franklin Co. Ozark Natl. For., Gray's Picnic Area on FSR 1003 (DAPC); Garland Co. Hot Springs (CUIC)(MCZ); Hempstead Co. Hope (MCZ); Pulaski Co. South West (AMNH); **Delaware**. New Castle Co. Newark (UASM); **D.C.** (CMNH)(USNM); Rock Creek (USNM); Rock Creek Pk. (USNM); Rock Creek Valley (USNM); Washington (CUIC)(USNM); **Florida**. Alachua Co. (FSCA); Gainesville (FSCA); Dixie Co. Pine Landing (UASM); Hernando Co. 9.7 km w Brooksville (FMNH); Liberty Co. Torreya St. Pk. (RHTC); **Georgia**. (IZWP); Atlanta (FMNH); **Illinois**. (CMNH); Alexander Co. Olive Branch (CAS)(FMNH); **Indiana**. Crawford Co. Grantsburg (FSCA); Jefferson Co. Madison (FSCA); Marion Co. Indianapolis (FSCA); St. Joseph Co. Pine (FMNH); **Kansas**. Shawnee Co. Topeka (USNM); Wyandotte Co. Argentine (AMNH); **Kentucky**. (AMNH)(CAS)(CMNH)(CUIC)(MCZ)(OSUC)(USNM); Christian Co. 8 km w Hopkinsville (DAPC); Henderson Co. Henderson (MZUM; Rowan Co. Morehead (CNC); **Louisiana**. St. Mary Co. Morgan City (MCZ); **Maryland**. (BMNH)(CMNH); Baltimore (CAS)(IZWP)(USNM)(ZSMM); Anne Arundel Co. Odenton (CUIC); Baltimore Co. Gunpowder (USNM); Calvert Co. Flag Ponds Nature Park (USNM); Harford Co. Edgewood (USNM); Montgomery Co. Colesville (MCZ); Glen Echo (USNM); Takoma Park (CAS)(DHK)(CNC); Prince Georges Co. Beltsville (FSCA)(USNM); Bladensburg (USNM); Branchville (USNM); College Park (FSCA); **Michigan** Monroe Co. Toledo Beach (USNM); **Mississippi**. George Co. Lucedale (CUIC); Harrison Co. Gulfport (CUIC); Perry Co. New Augusta (CUIC); Smith Co. 3.7 km e Polkville (RHTC); County? Lakesville (CUIC); County? R.F. Laird Agr. Co. (CUIC); **Missouri**. St. Louis (CAS)(MCZ)(USNM); **Montana**. Gallatin Co. West Yellowstone (CAS); **Nebraska**. Lancaster Co. Malcolm (FMNH); **New Jersey**. Camden Co. Grenloch (OSUC); Cape May Co. Ocean City (AMNH); Monmouth Co. Englishtown (FMNH); **North Carolina**. (MCZ); Buncombe Co. Weaverville (USNM); Catawba Co. Hog Hill (CMNH); Cleveland Co. Shelby (CNC); Duplin Co. West (CMNH); Durham Co. Durham (CDAE); Mecklenburg Co. Charlotte (CNC); Moore Co. Southern Pines (CAS); Wake Co. Raleigh (BMNH)(CNC); **Ohio**. (AMNH)(CAS)(MCZ)(MPMM)(USNM); Clermont Co. (AMNH); Clinton Co. (OSUC); Crawford Co. Plankton (CAS); Delaware Co. (OSUC); Franklin Co. Columbus (OSUC); Hamilton Co. Cincinnati (BMNH)(CAS)(MCZ)(USNM); Hocking Co. (OSUC); **Oklahoma**. Latimer Co. (FSCA); 8 km w Red Oak (FSCA)(UASM); **Pennsylvania**. (OSUC); Allegheny Co. (CMNH)(CUIC); Pittsburgh (CMNH); Bucks Co. Tinicum Is. (USNM); Delaware Co. Broomall (AMNH); Chadds Ford (JEWC); Lansdowne (AMNH); Upper Darby (USNM); Westmoreland Co. Jeanette (CMNH); **South Carolina**. Beaufort Co. (USNM); Oconee Co. 8 km n Oconee St. Pk., Sumter National For. (DHK); Pickens Co. Clemson College (USNM); Spartanburg Co. Camp Croft (FMNH); **Tennessee**. (MCZ); Davidson Co. Nashville (MCZ); Knox Co. Knoxville (CNC); Obion Co. Reelfoot Lake, Horse Island (DAPC); Sevier Co. Gatlinburg (CNC); **Texas**. (BMNH)(MCZ); Colorado Co. Columbus (USNM); Gonzales Co. Palmetto State Park (CMNH); Harris Co. Houston (USNM); Nacogdoches Co. Nacogdoches (CNC); **Virginia**. Falls Church (CAS)(USNM); Richmond (USNM); Alex Co. (MCZ)(USNM); Fairfax Co. (CMNH); Gt. Falls (USNM); Mt. Vernon (CAS)(USNM); Fauquier Co. Belvoir (USNM); Lee Co. Jone's Creek (MCZ)(USNM); Pennington Gap (USNM); Loudoun Co. Lucketts (USNM); Nelson Co. (USNM); Shipman (USNM); Prince William Co. Occoquan (USNM); Not located "Ash Grove" (CUIC) and "Veitch" (USNM). **West Virginia**. Nicholas Co. nr. Summersville (CMNH).



MAP 19. Geographical distribution of *Coptodera aerata* Dejean. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

No or mixed labels (BMNH)(CAS)(IZWP)(MCZ). Collections in all months of the year except for March and December.

Coptodera waytkowskii Liebke
Figs. 33D, 34G & 34H; Map 20

Coptodera waytkowskii Liebke 1951: 243. Type material: HOLOTYPE, male, labelled: PERU Satipo, x-xii 1935, F. Waytkowski, B.M. 1936-732; Sammlung, M. Liebke (light green paper); Type (pink paper); Coptodera waytkowskii Lbk. M. Liebke determ. Type; Inst. Zool. P.A.N. Warszawa 31/54 [IZWP]. Type locality: Satipo, Junín dept., Peru.

Description.-- Character states of the *C. aerata* group and the following. See Tables II, IV, and VI for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head rufo-testaceous to rufo-brunneous; pronotum lighter, testaceous to rufo-testaceous; elytra brunneo-testaceous to brunneous with faint to moderate aeneous lustre and testaceous preapical markings, lateral margin testaceous to rufo-testaceous; mouthparts, antennae, and legs testaceous to rufo-testaceous. Ventral surface testaceous to brunneous.

Head. Fine setae between posterior pair of supraorbital setae.

Elytra (Fig. 33D). Interneurs finely punctate.

Male genitalia. As in Figs. 34G-34H, median lobe with membranous portion medium-short. Apical portion medium-short, flattened, in lateral aspect trianguloid, moderately broad, tapered gradually toward apex, in dorsal aspect broad, hardly tapered; apex in lateral aspect narrowly rounded, in dorsal aspect broadly rounded. Internal sac spine A small; spine group B with one small spine; spine group C with two small spines.

Notes about habitat.-- None available.

Geographical distribution (Map 20).-- This species is known only from the Amazon Basin of South America, in eastern Brazil and eastern Peru.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for *C. aerata* above, the postulated adelphotaxon of *C. waytkowskii.*

Material examined.-- We examined 3 specimens, including the holotype, and saw non-type material from the following localities:
BRAZIL Para. (CMNH);
PERU Junín. Satipo (IZWP);

Coptodera erwini, new species
Fig. 33E; Map 20

Type material.-- HOLOTYPE, female labelled: PERU: MADRE DE DIOS Pakitza, Zone 02 16Sept88 T.L.Erwin & B.D. Farrell Colls 12°07'S 70°58'W; Insecticidal Fog Canopy/Celtis BIOLAT 02131512; BIOLAT/COLE 000008471 [USNM].

Type locality.-- Pakitza, department of Madre de Dios, Peru.

Derivation of specific epithet.-- This is the Latinized surname of Terry L. Erwin, who has collected many fine carabids from the forest canopy, including the type specimen of this species, using his fogging technique. He has also collected many specimens of other *Coptodera* species in Central and South America.

Description.-- Character states of the *C. aerata* group and the following. See Tables III, V and VII for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum rufo-testaceous; elytra rufo-testaceous in basal half, dark brunneous in apical half; lateral margin of elytron rufo-testaceous; appendages, antennae and

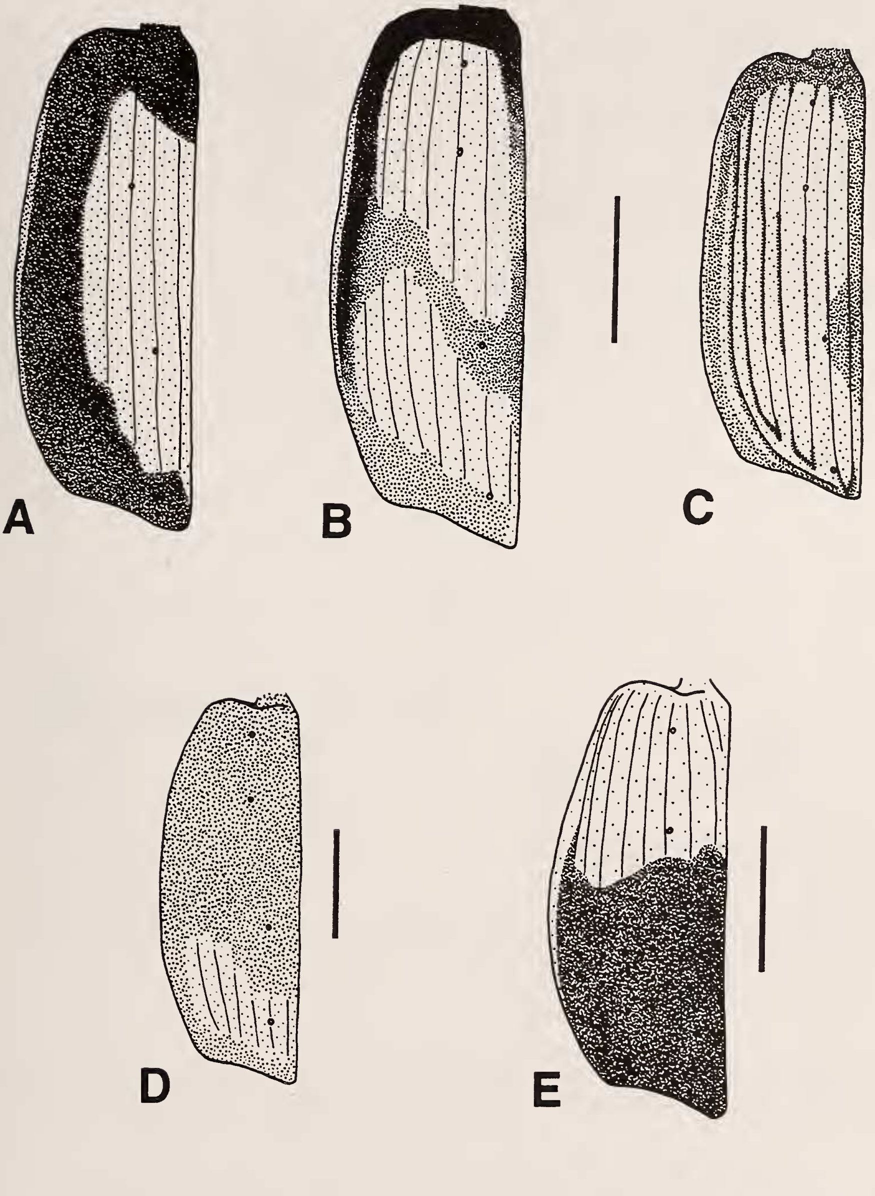


FIGURE 33. Line drawings of left elytron of *Coptodera aerata* group, dorsal aspect. Figs. A-C: *C. nitidula* (Buquet). Fig. D: *C. waytkowskii* Liebke. Fig. E. *C. erwini*, new species. Scale bars = 1 mm.

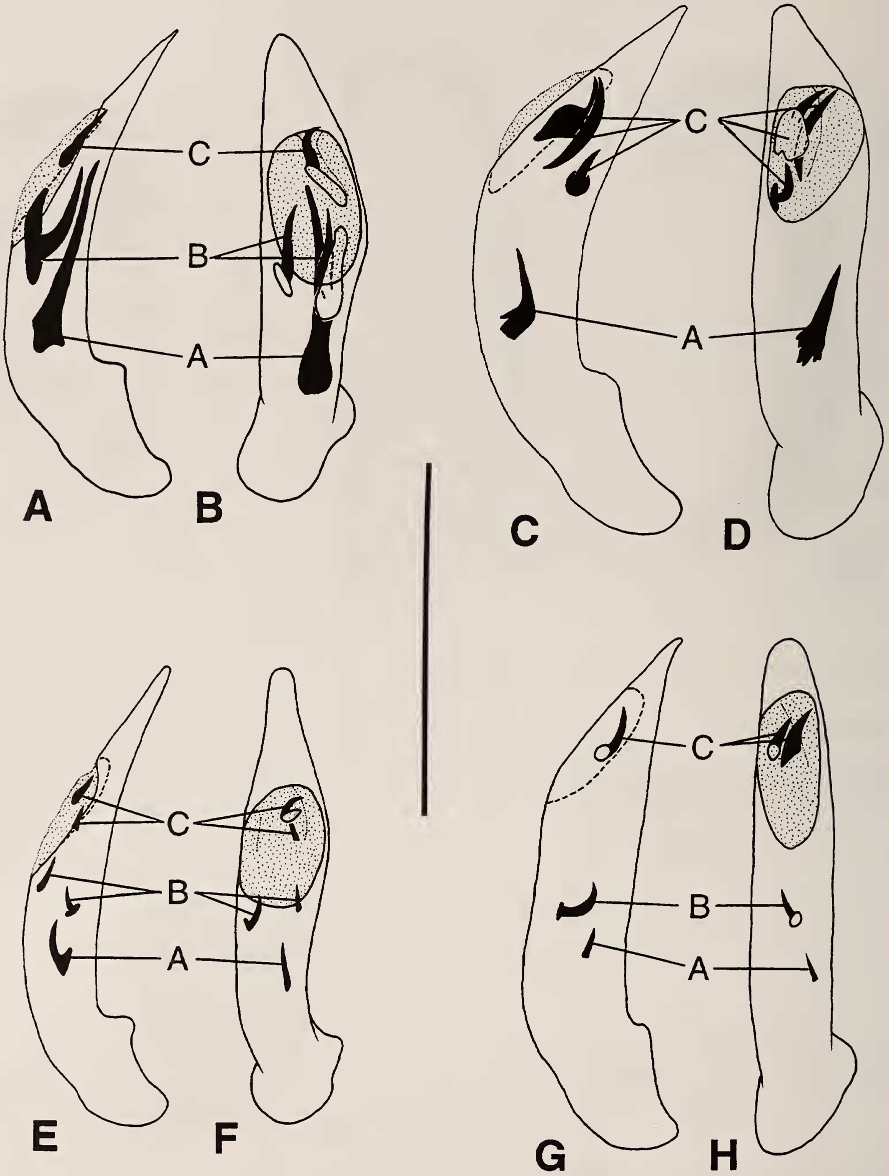
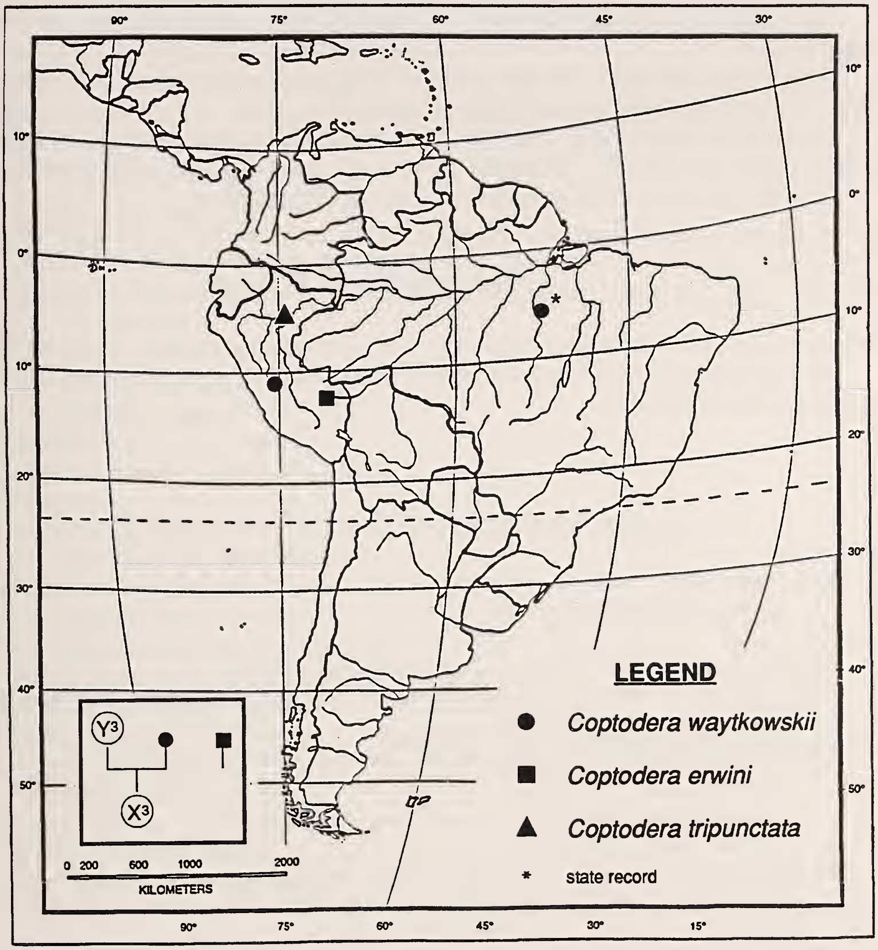


FIGURE 34. Line drawings of male genitalia of *Coptodera aerata* group. Figs. A, C, E & G left lateral aspect. Figs. B, D, F & H dorsal aspect. Figs. A-B: *C. nitidula* (Buquet). Figs. C-D: *C. brunnea*, new species. Figs. E-F: *C. aerata* Dejean. Figs. G-H: *C. waytkowskii* Liebke. Scale bars = 1 mm. Legend: A, spine A; B, spine B; C, spine C.



MAP 20. Geographical distribution of *Coptodera waytkowskii* Liebke, *C. erwini*, new species and *C. tripunctata*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

mouthparts rufo-testaceous. Ventral surface of head and prothorax rufo-testaceous, mesepimeron and mesepisternum slightly darkened; metepisternum, metepimeron, metasternum and abdominal sterna rufo-piceous; metasternum slightly lightened medially (elytral epipleuron rufo-testaceous).

Elytra (Fig. 33E). Interneurs impunctate.

Male genitalia. Unknown.

Notes about habitat.-- The type specimen was taken from the canopy of *Celtis* L. by fogging with an insecticide.

Geographical distribution (Map 20).-- This species is known only from the type locality in southern Peru.

Chorological affinities.-- The type specimen of this species and specimens of *C. nitidula* were both collected at the same time at Pakitza, Madre de Dios, Peru.

Phylogenetic relationships (Fig. 36).-- The position of this species is unresolved due to the lack of a male specimen; it is tentatively placed at the end of the *C. aerata* group lineage.

Material examined.-- Type material only, see above for details.

Species *Incertae Sedis*

Coptodera deplanata Motschulsky 1864: 223. Type material: not located. Type area: Brazil.

No type specimen could be located, and the description is not clear as to whether or not this species is even a *Coptodera*.

Checklist of New World Species of *Coptodera*[1]

sallei group
    sallei, new name. Guatemala, México
        variegata Chaudoir 1869: 168
elongata group
    elongata Putzeys 1845: 395. Costa Rica, Guatemala, México
    schaumi Chaudoir 1861: 123. Brazil, Colombia?, Costa Rica, Guatemala, Nicaragua, Panamá
        bifasciata Schaum 1860: 191
    megalops Bates 1869: 77. Bolivia, Brazil, Colombia, Ecuador, Peru
        batesi Chaudoir 1869: 172
        pertzeli Liebke 1951: 242
        peruana Liebke 1951: 243
    championi Bates 1883: 180. Colombia, Panamá, Nicaragua
    apicalis new species. Colombia, Ecuador
aurata group
    xanthopleura Bates 1891: 270. México
    aurata Chevrolat 1835: No. 162. México, Guatemala
    viridis new species. México
depressa group
    depressa Dejean 1831: 393. Argentina, Brazil, Colombia, Paraguay, Peru
        undulata Perty 1830: 5
        plaumanni Liebke 1939: 127
    versicolor Bates 1869: 76. Bolivia, Brazil, Colombia Ecuador, Peru, Venezuela
        affinis Chaudoir 1869: 168

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[1] Synonyms in italics

- transversa group
  - dromioides (Bates) 1869: 79. Brazil, French Guiana
    - *corticalis* Chaudoir 1869: 207
  - nigrosignata (Chaudoir) 1869: 206. Brazil
  - fulminans (Bates) 1869: 78. Brazil
  - nigrostriata (Reiche) 1843: 179. Bolivia, Brazil, Colombia, Peru, Venezuela
    - *multiguttata* Putzeys 1845: 377
    - *variegata* Chaudoir 1848: 117
    - *pallida* Bates 1869: 78
  - lineata (Bates) 1883: 184. Costa Rica, Guatemala, México, Nicaragua, Panamá
  - stockwelli, new species. Panamá
  - transversa (Reiche) 1843: 179. Bolivia, Brazil, Colombia, Costa Rica, Guatemala, México, Panamá
    - *atriceps* Bates 1869: 78
    - *picturata* Chaudoir 1869: 205
    - *undulata* Chaudoir 1869: 206
  - sigillata, new species. Brazil
  - squiresi (Chaudoir) 1869: 201. Brazil
- festiva group
  - sahlbergi Chaudoir 1869: 181. Argentina, Bolivia, Brazil, Paraguay
    - *discicollis* Chaudoir 1869: 181.
  - relucens Bates 1869: 73. Brazil
    - *lebioides* Bates 1869: 74
    - *rotundipennis* Chaudoir 1869:182
  - poecila Bates 1883: 183. Panamá
  - pakitza, new species. Peru
  - festiva Dejean 1825: 274. Brazil, Costa Rica, Cuba, Guatemala, Haiti, Jamaica, México, Panamá
    - *chloris* Bates 1883: 182
    - *chalcoptera* Chaudoir 1869: 184
  - foveolata new species. México
  - nigroviridis new species. México
  - rufescens Buquet 1835: 617. French Guiana, Brazil
    - *luteopicta* Chaudoir 1850: 363
  - teutonica, new species. Brazil
- aeneorufa group
  - aeneorufa Bates 1869: 76. Bolivia, Brazil, Ecuador, Surinam
- bifasciata group
  - bifasciata Putzeys 1845: 394. Bolivia, Brazil, Venezuela
  - tripartita Chaudoir 1869: 180. Brazil
  - cupreotincta Bates 1869: 73. Bolivia, Brazil, Costa Rica, México, Nicaragua, Panamá, Peru
    - *tesselata* Chaudoir 1869: 199
    - *amazonica* Chaudoir 1869: 200
  - braziliensis new species. Brazil
- emarginata group
  - chalcites Bates 1869: 75. Brazil, Ecuador, Peru
    - *aeneocuprea* Chaudoir 1869: 177

emarginata Dejean 1825: 276. Brazil
    aenea Buquet 1834: 673
acutipennis (Buquet) 1834: 674. Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guatemala, México, Nicaragua, Panamá, Peru, Trinidad
    spinipennis Bates 1869: 75
    scintillans Bates 1878: 604
picea group
picea Dejean 1826: 458. Belize, Bolivia, Brazil, Colombia, Cuba, Guatemala, Guyana, Honduras, México, Nicaragua, Panamá, Paraguay, Peru, Surinam, Trinidad, Venezuela, United States
    velox Gory 1833: 195
    rufula Buquet 1834: 680
    unicolor Chevrolat 1834: No. [40]
    obscura Laporte 1834: 51
aerata group
nitidula (Buquet) 1834: 677. Argentina, Bolivia, Brazil, Costa Rica, Ecuador, French Guiana, Guatemala, Guyana, México, Nicaragua, Panamá, Paraguay, Peru, Surinam, United States
    triangularis Buquet 1834: 678.
    luculenta Erichson 1847: 69
    debilis Bates 1869: 76
    flavodisca Chaudoir 1869: 187.
    nubiculosa Chaudoir 1869: 186.
    flavodisca immaculipennis Bates 1883: 182.
brunnea new species. Belize, México, United States
aerata Dejean 1825: 277. United States
    viridipennis Gory 1833: 194
    viridipennis LeConte 1848: 196
    ruficornis Chaudoir 1869: 179
waytkowskii Liebke 1951: 243. Brazil, Peru
erwini, news species. Peru

tripunctata, new species. Peru
species *incertae sedis*
deplanata Motschulsky 1864: 223. Brazil

Misplaced Species

Eucalyptocola marcida Blackburn 1903: 91. HOLOTYPE female, glued to card on which is written T. Nels.V. 7/89 ("T." in black print, remainder in red print); Type (disc ringed with red); Blackburn Coll 1910-236; Eucalyptocola marcida Blackb (handwritten); Coptodera marcida Blackb /87 det. George E. Ball; Microlestodedes marcida Blackbn det B.P. Moore 1987 [BMNH].-- Sloane 1907: 376,377.

Sloane (1907) transferred this species to the genus *Coptodera*. At the authors' request, B.P. Moore confirmed that the type specimen in question was not a member of *Coptodera*, and identified it as a member of *Microlestodes* Baehr.

Coptodera philippinensis Jedlička 1935: 116. HOLOTYPE male, glued to card, and labelled: Type (disc ringed with red); Philippine Is. Coll. Bottcher. B.M. 1929-201; Coptodera philippinen-type sis sp.n. Det.ING.JEDLIČKA (first three lines handwritten; salmon-colored paper); 217 (handwritten); Coptodera philippi -ensis ♂ Jedl. det. George E. Ball /87 [BMNH].

This specimen is a member of the metallicine genus *Anchista* Nietner. Accordingly, it is transferred herewith.

Coptodera robusta Bates 1884: 296. HOLOTYPE female, labelled: Type H.T. (disc ringed with red); Costa Rica Van Patten.; B.C.A. Col. I.1. Coptodera robusta Bates; Coptodera robusta Bates (in Bates' handwriting); HOLOTYPE ♀ Coptodera robustus Bts. By Erwin '76 [BMNH].

This specimen is a member of the subgenus *Phloeotherates* Bates, in the genus *Stenognathus* Chaudoir. Accordingly, it is transferred, herewith.

Coptodera polygona Bates 1869: 72. LECTOTYPE female, here selected, labelled: Ega; polygona Bates; Lelis bifasciata Chaud; Ex Musaeo H.W. Bates 1892; LECTO- TYPE (disc ringed with purple); LECTOTYPE Coptodera polygona Bts. det. George E. Ball '72 [MNHP].

This specimen is a member of the genus *Lelis* Chaudoir, and is transferred accordingly, herewith.

Coptodera latipennis Bates 1869: 72. HOLOTYPE female, labelled: S. Paulo Amaz (handwritten); latipennis Bates (handwritten); Ex Musaeo H.W. Bates 1892; HOLO (red paper); TYPE (red paper); latipennis Bates Ent M. M. July 1869; Museum Paris ex Coll R. Oberthür (light green paper); HOLOTYPE Coptodera latipennis Bates det. George E. Ball '72 [MNHP].

This specimen is a member of the genus *Lelis* Chaudoir, and is transferred accordingly, herewith.

Coptodera rutila Bates 1869: 75. LECTOTYPE female, labelled: Ega; rutila Bates; 702 (blue paper); Lelis viridipennis Chaud; TYPE (red paper); LECTO TYPE (disc with purple border); LECTOTYPE Coptodera rutila Bates det. George E. Ball '72 [MNHP].

This specimen is a member of the genus *Lelis* Chaudoir, and is transferred accordingly, herewith.

Species Names With New Status

Coptodera chaudoiri Andrewes, NEW STATUS

Coptodera transversa Schmidt-Goebel 1846: 54 (*nec* Reiche). Type material not seen. Type area: Burma.

Coptodera bicincta Chaudoir 1869: 187 (*nec* Hope). Type material: not seen. Type area: Hong Kong.

Coptodera interrupta Bates 1892: 411 (*nec* Schmidt-Goebel). Type material: not seen. Type area: Burma.

Coptodera chaudoiri Andrewes 1919: 179. Type material: not seen. Type area: Hong Kong.

Coptodera transversa Schmidt-Goebel is a junior primary homonym of *C. transvera* Reiche 1843: 179. *C. bicincta* Chaudoir (1869: 187) is not available, as it is a junior primary homonym of *C. bicincta* Hope (1845: 15) which is presently in *Somotrichus* Seidlitz. *C. interrupta* Bates (1892: 411) also is not available, as it is a junior primary homonym of *C. interrupta* Schmidt-Goebel (1846: 53). *Coptodera chaudoiri* Andrewes is the valid name for this species.

Coptodera fasciolata Macleay, NEW STATUS

Scopodes auratus Macleay 1871: 92 (*nec* Chevrolat). Type material: not seen [ANIC]. Type locality: Gayndah, Queensland, Australia.

Ectinochila tesselata Chaudoir 1883: 22 (*nec* Chaudoir 1869). Type material: not seen [MNHP]. Type area: Queensland, Australia

Scopodes fasciolatus Macleay 1887: 219. Type material: not seen [ANIC]. Type locality: Cairns, Queensland, Australia.

Sloane (1907: 381) synonymized the latter two names with *Coptodera aurata* Macleay (1871: 92) as the senior synonym. However, *C. aurata* Macleay is a junior primary homonym of *Coptodera aurata* Chevrolat (1835: 162). *Ectinochila tesselata* Chaudoir (1883: 22) normally would be the next available name, but it is a junior primary homonym of *Coptodera tesselatus* Chaudoir (1869: 199). The next available name, *Scopodes fasciolatus* Macleay (1887: 219), is not pre-occupied, and *Coptodera fasciolata* Macleay is the valid name for this species.

Ecological Considerations

This section is presented both to summarize information about aspects of the natural history of the New World species of *Coptodera*, and to provide a background for seeking the adaptive significance of the structural features of the species—a topic that is treated in the following sections. The evidence available is incomplete and anecdotal, consisting of rather casual or standard observations made and recorded in the course of collection of specimens.

All known species of *Coptodera* are forest inhabitants, with most species confined to the tropics between sea level and 2300 m altitude, and most species associated directly, and evidently for their entire lives, with trees. Erwin (1979b) classifies their habitat as "tree trunks and limbs" (p. 560), and as "logs, surface" (p. 584). Evidently, adults (and probably larvae) are predators on arthropods that live under bark or on standing or fallen tree trunks and branches (Bates 1869: 69).

Collection records, for specimens representing seven species groups at u-v light traps, provide evidence that adults fly, and that they are night-active. Adults of all of the New World species, in fact, are macropterous, with body proportions appropriate for flight (*i.e.*, elytra about 60 percent of the total length of body [cf. Frontispiece]).

Additional evidence for nocturnal activity is direct observation (by the authors and several colleagues) of adults of various species being seen at night on logs and at fruitfalls.

Association of some species (*Coptodera acutipennis* and *C. festiva*) with fruitfalls in tropical forest shows that foraging by adults is not confined to the vegetative parts of plants. In fact, adults of *C. acutipennis* have been taken principally at fruitfalls (seven collections), and only on the ground (excluding captures at light traps).

Local distribution of *Coptodera* seems to be patchy, and a correlate of trees in a suitable state of decomposition (*i.e.*, with bark loosened to some extent), or a correlate of occurrence and location of fruitfalls. Probably the under-bark habitats provide the resources required for only a single generation to be produced at each site. Thus, maintenance of dispersal ability among adults would be essential, and hence natural selection would favor the maintenance of flight capability.

Probably fruitfalls are only sources for feeding by adults, the latter eating maggots and other small saprophagous animals that are attracted to the fruit. Exploitation of fruit falls, because of their disjunct occurrence, would be achieved most readily by insects with flight ability.

TABLE XI. Sympatric assemblages of *Coptodera* species in the Neotropical Region.

Locality	Site	Species
MEX. Veracruz, 4 km W. Sontecomapan, 30 m IV.3-16.1966	Lowland evergreen forest, under bark	*elongata*, *aurata*, and *lineata*
SAME	SAME	*elongata*, *lineata*, *transversa*, and *picea*
MEX. Chiapas, 7.4 km N. Frontera-Comalapa, 732 m IX.2.1967	SAME	*xanthopleura*, *aurata*, and *cupreotincta*
MEX. Oaxaca, Rte. 175, 9 km S.Valle Nacional, 660 m VII.30.1972	Montane evergreen forest, under bark (of single fallen log)	*elongata*, *aurata*, and *cupreotincta*
PAN. Canal Zone, nr. sea level V- VII	Lowland evergreen forest, on logs and under bark	*championi*, *transversa*, *stockwelli*, *cupreotincta*, and *nitidula*
PAN. C.Z., Madden Dam for., nr. sea level VI.30.1972	Lowland evergreen forest, on logs	*championi*, *stockwelli*, and *cupreotincta*
PERU. Madre de Dios Pakitza 10°55'S, 71°35'W IX.10.1989	Lowland evergreen forest, running on logs	*megalops*, *versicolor*, and *chalcites*
SAME, but: 12°07'S, 70°58'W X.29-XI.01.1990	SAME	*aeneorufa*, *pakitza*, and *cupreotincta*

Among the species of *Coptodera*, requirements for life seem to overlap broadly, as indicated by occurrence of several species in the same habitats at the same time of year. The evidence for co-occurrence is presented in Table XI. Co-occurrence provides the potential for competition and genetic exchange among related species. No evidence is available for either of these phenomena in *Coptodera*.

Evolutionary Considerations

In this section, a reconstructed phylogeny is presented, based on analysis of structural features of *Coptodera* and its putative relatives. The resulting system of hypotheses is combined with an analysis of geographical distribution to provide an outline of the geographical history of the genus in the New World.

Reconstructed phylogeny

Methods.-- Our general approach to phylogenetic reconstruction, the "qualitative Hennigian method", is described in a passage by Saether (1990: 107) that also contrasts this method with the presently more widely used methods of quantitative phyletics or neocladistics: "In the qualitative Hennigian method, the parsimony criterion is used when choosing among alternative hypotheses of explanation of single character distribution. The selection and interpretation equals the cladogenetic analysis [or the search for adelphotaxa]. In neocladistic methods the parsimony criterion is used to find the tree implying the fewest evolutionary gains and losses with the fewest lines. The explanation of characters enters as an afterthought".

In more detail, the phylogeny of *Coptodera* was reconstructed in part by character analysis, and in part by attempting to discover and rationalize in an evolutionary framework the various groupings that were discovered by taxonomic analysis. For example, we recognized groups based on color, genitalic form and armature (or lack of it) in the internal sac, lobing of the posterior margin of the pronotum, and overall size. We found that such groups could be organized into two complexes, based on a combination of number of setae (or setigerous punctures) in elytral interval 3, and notching of the middle tibiae of males. We sought evidence to support these groupings, and to determine the pattern of adelphotaxon relationships.

Detailed character analysis was by outgroup comparison for initial polarization of character states, as explained by Ross (1974: 151-156), Wiley (1981: 139-146), Watrous and Wheeler (1981), and Maddison *et al.* (1984). We used also group trends, as explained by Ross (1974: 156). The direction of evolution of other characters was determined after a general pattern was perceived, by examining the pattern of distribution of states on a preliminary reconstruction of the phylogeny (a method designated character correlation by Hennig [1966] and by Ekis [1977], and the "functional outgroup/functional ingroup" method of Watrous and Wheeler [1981]. See also Ball and Maddison [1987: 258-259]). Characters were not weighted formally, but the features of the male genitalia and mandibles were analyzed in considerable detail.

Autapotypic and synapotypic character states are indicated in Table XII and in Figs. 35 and 36 by number, and are sequenced by letters and superscript numbers and letters. Postulated losses and reductions are indicated by a superscript minus sign. For characters with two or more apotypic states, each is designated by a different lower case letter, if each was postulated to be derived separately from the plesiotypic condition, thus forming a branched transformation series. If the apotypic states were postulated to form an unbranched transformation series, each state was labelled with the same letter but with a different number, implying direction of change (*i.e.*, a1, a2, a3). Character states postulated to represent reversals are indicated by a superscript "R". Stages in reversal were indicated by a number associated with superscript "R".

States of characters 12 and 28 were designated by their group-specific patterns. Group or lineage membership was indicated by a lower case letter.

For characters 13, 16, 46, 47, and 48, the variation pattern was so erratic that it was impossible to group them *a priori* in transformation series. Accordingly, apotypic states were designated simply by positive and negative numbers, indicating postulated distance and direction from the plesiotypic condition.

Other methods of phylogenetic analysis.-- See Appendix B for a synopsis of results of a numerical cladistic treatment of the data in Table XII.

Taxa studied.-- We examined representatives of: *Somotrichus unifasciatus* Dejean, and several species of *Pericalus* Macleay: *figuratus* Chaudoir, *undatus* Chaudoir, *signatus* Jedlička, *levifrons* Heller, *ornatus* Schmidt-Göbel, *cicindeloides* MacLeay, *amplus* Andrewes, and *tetrastigma* Chaudoir. Because of extensive parallelism in structural features between members of *Coptodera* and *Pericalus*, and because of extensive parallelism between Old World and New World assemblages of *Coptodera*, we used *Somotrichus* as functional outgroup. We regard this genus as representing the most primitive assemblage of the subtribe Pericalina because of details of stylomere 2 of the ovipositor, which lacks a pronounced basal lobe, has three ensiform setae (two lateral, one medial), and has a pair of nematiform setae each inserted in a single ventral preapical sensory pit (Ball and Shpeley 1983: 748, Figs. 2a-c [cf. Figs. 3a-7c]). Basilewsky (1984: 552-553) places the somotrichoid assemblage in a group of its own, separate from the Pericalina, an arrangement that is consistent with our postulate, as long as somotrichines and pericalines (*sensu* Basilewsky) are regarded as adelphotaxa of one another.

Monophyly of the New World species of *Coptodera*.-- Jeannel (1949: 924) designated the New World species as the only members of *Coptodera*, and included the Old World species of the complex in other genera. Although we do not accept that *Coptodera* is a New World precinctive genus, for the purposes of phylogenetic analysis and in the absence of evidence to the contrary, we proceed as if all of the New World species are derived from a common ancestor that itself was a New World resident.

Phylogenetic analysis of the male genitalia of *Coptodera*.-- This analysis was difficult because of the extensive variation of these structures, not only between species that are postulated on other grounds to be related, but within at least one species (*C. acutipennis*). Some features were analyzed easily for the species assemblage as a whole (position of the ostium, size of the membranous portion of the median lobe, presence or absence of armature of the internal sac, and spine groups of the internal sac), but other features had to be analyzed in terms of the species groups (aspects associated with form and shape, and details of pattern of spination). Thus, we recognize five basic types, based on their overall size and general appearance: the *elongata* type (designated by "e"), characteristic of the *C. sallei*, *elongata*, and *aurata* species groups; the *depressa* type ("d"), characteristic of the *C. depressa* group; the *transversa* type ("t"), characteristic of the *C. transversa* group; the *festiva* type ("f"), characteristic of the *C. festiva*, *aeneorufa*, *bifasciata*, and *emarginata* groups; the *picea* type ("p"), characteristic of *C. picea*; and the *aerata* type ("a"), characteristic of the *C. aerata* group. Details are provided below.

Phylogenetic designation of character states.-- Each character is listed by number in sequence of its appearance in the reconstructed phylogeny (Figs. 35 and 36). Below, for each character, we note character states and the basis for their designation as plesiotypic or apotypic. See Table XII for details of character state distribution.

Character 00. Legs, tarsal claws: plesiotypic, inner margins smooth; apotypic, inner margins pectinate. See also character 50. Basis for designation: outgroup comparison.

Character 01. Labium: seta on palpiger. Two states: plesiotypic, asetose; apotypic, palpiger with single long seta (Fig. 6A, p). Basis for designation: outgroup comparison.

Character 02. Mentum, tooth. Two states: plesiotypic, dentate; apotypic, 02^-, edentate (Figs. 6A-D). Basis for designation: outgroup comparison.

Character 03. Ovipositor, stylomere 2, nematiform setae. Three states: plesiotypic, setae relatively long; apotypic, setae short (Fig. 12H, ns); apotypic, 03^-, setae absent. Basis for designation: outgroup comparison.

Character 04. Stylomere 2, microspinules. Two states: plesiotypic, absent; apotypic, present. Basis for designation: outgroup comparison.

Character 05. Elytra, discal setigerous punctures. Two states: plesiotypic, non-foveate; apotypic, foveate. Basis for designation: outgroup comparison.

Character 06. Elytron, number of discal setae. Two states: plesiotypic, four; apotypic, 06^-, three. Basis for designation: outgroup comparison.

Character 07. Ovipositor, stylomere 2, position of ensiform setae. Two states: plesiotypic, setae on dorsal margin; apotypic, setae lateral (Fig. 12A). Basis for designation: outgroup comparison.

Character 08. Labrum, anterior margin. Two states: plesiotypic, smooth, or shallowly emarginate; apotypic, narrowly, deeply emarginate (Figs. 1C-D). Basis for designation: outgroup comparison.

Character 09. Median lobe, position of ostium. Five states: plesiotypic, pleuropic-left (Figs. 19A-D); apotypic, 09^{a1}, left pleuropic-catopic, more pleuropic than catopic (Figs. 14B-C); apotypic, 09^{a2}, left pleuropic-catopic, more catopic than pleuropic (Figs. 16A-J); apotypic, 09^{b1}, anopic (Figs. 34A-H), and pleuropic-right, 09^{b2} (Figs. 28E-F).

Outgroup comparison indicates the anopic position as plesiotypic. However, within the New World taxa of *Coptodera*, the anopic position characterizes only the generally derived *picea-aerata* lineage. Thus, character correlation suggests that the anopic position is derived. Expressed in another way, with the *C. aeneorufa* group (lineage D^3, Figs. 35 and 36) as functional outgroup for lineage E^3, the left pleuropic-catopic position is seen as plesiotypic. What is known about genitalic structure and character trends for carabids in general, however, leads us to believe that the catopic condition is likely to be an end-point rather than a beginning.

The pleuropic-right position of the ostium is confined to another moderately derived lineage (F^3, Figs. 35 and 36). This leaves pleuropic-left as the position of choice for the plesiotypic condition: it is characteristic of the less derived *C. depressa* and *transversa* groups of lineage R.

With pleuropic-left as plesiotypic, we postulate change of position of the ostium in two directions: a, toward catopic; and b, to anopic, then to pleuropic-right (Fig. 39).

Character 10. Dorsal surface, luster. Three states: plesiotypic, dull; apotypic, shining; apotypic, dull, R-. Basis for designation: outgroup comparison and character correlation (the reversal).

Character 11. Male genitalia, armature of the internal sac. Three states: plesiotypic, without armature; apotypic, 11^{a}, with patch of microspines (Figs. 14B-C); apotypic, 11^{b}, with assemblage of macrospines (see, for example, Figs. 24A-P). Character state b is analyzed in detail as characters 46, 47, and 48. Basis for designation: outgroup comparison.

Character 12. Male genitalia, form of the median lobe. Analysis is in terms of a general pattern of form. See figures.

The *elongata* form (Figs. 14B-C, 16A-J, and 17A-F). Median lobe short and thick, apical portion short overall, of various widths (12e). In lateral aspect, apical portion rather broad, tapered to narrowly rounded apex, $12e^{a1}$ (Figs. 14B, 16A and C); apotypic, apical portion narrowed, triangular, $12e^{a2-}$ (Fig. 16E); apotypic, apical portion narrowed, subulate, $12e^{a3-}$ (Figs. 17A, C and E); apotypic, apical portion shortened and widened, $12e^{a2+}$ (Figs. 16G and I).

Within this complex, *C. xanthopleura* has an unusually slender median lobe, which could be an ancestral form. However, because of character correlation, we believe that this form is secondary, and thus is derived. It is designated $12e^{R}$.

The *depressa* form (Figs. 18A-D). Median lobe slender, with apical portion slender, of moderate size. The only difference between the two species is in distribution of the extensive membranous area (12d).

The *transversa* form (Figs. 21A-P, 22A-B). Median lobe slender, elongate, with apices of varying sizes, designated as follows. Plesiotypic, gradually curved ventrally, apical portion short and tapered to a narrowly rounded apex (12t). Apotypic states of apical portion ($12t^{a1}$

Fig. 21A) and still longer and curved ($12t^{a2}$, Fig. 21G); and apical portion much shorter and broader ($12t^{b-}$, Figs. 21I, K, and 22A-B).

The median lobe of the *festiva* form is slender with the apical portion of various lengths. Based on character correlation and outgroup analysis (with the *depressa* group as functional outgroup, lineage S, Figs. 35 and 36), the apical portion of moderate length is postulated to be plesiotypic (12f, Figs. 24A-B, 24I-J, and 25A-B). There are three apotypic forms, characterized by increasing length of the apical portion: $12f^{a1}$,(Figs. 24E-F, 24K-L, 27A-B, 27E-F, and 28E-F); $12f^{a2}$, (Figs. Figs. 24C-D, O-P); $12f^{a3}$ (Figs. 27C-D, and 27G-H); and $12f^{a4}$ (long and spatulate, Figs. 24M-N). One apotypic form is postulated to be a reduction or loss, by shortening of the apical portion ($12f^{b-}$, Figs. 24G-H, and 28C-D); and one taxon, *C. acutipennis*, has states that extend from $12f^{a2}$ to $12f^{b-}$ (Figs. 29A-P, 30A-L, and 31A-B).

The *picea* form of median lobe (Figs. 32A-B) is slender, with a long apical portion and the apex curved at tip (12p).

The *aerata* form of median lobe is various in lateral aspect, and broader than usual in dorsal aspect, in those species with a prominent apical portion (*C. aerata*, *nitidula*, and *brunnea*, Figs. 34A-F). By character correlation (trends for reduction in spines of the internal sac and in size of the membranous portion of the median lobe) we postulate as plesiotypic (12a) the *aerata* type of median lobe, with moderately broad and fairly long apical portion. The *nitidula-brunnea* type is apotypic ($12a^{a}$) in the somewhat shortened and broadened apical portion. The median lobe of *C. aerata* is postulated to be apotypic ($12a^{bi-}$) by reduction in width of the apical portion in dorsal aspect, a trend carried to *C. waytkowskii*, with the apical portion shortened markedly ($12a^{b2-}$).

Character 13. Male genitalia, median lobe, extent of dorsal membranous area. Five states: plesiotypic, size moderate (as in Figs. 16C-F, and 17A-D); apotypic, larger, 13^{1} (Figs. 19A-D); and smaller, 13^{1-} and 13^{2-} (Figs. 21E-H, and 22A-B); and reversal to moderate size, 13^{R-} (Fig. 21C-D). Basis for designation: outgroup comparison.

Character 14. Pronotum, lateral margins. Three states: plesiotypic, narrow; apotypic, wide; apotypic, narrow, 14^{R-}, reversal, loss. Basis for designation: outgroup comparison and character correlation.

Character 15. Elytral disc, microsculpture, mesh pattern. Three states: plesiotypic, isodiametric; apotypic, transverse; and apotypic, isodiametric, 15^{R-}, reversal. Basis for designation: outgroup comparison and group trends in Carabidae, for postulation of the plesiotypic condition; character correlation for postulation of the reversals.

Character 16. Elytral intervals, form. Three states: plesiotypic, all intervals convex; apotypic, 16^{1-}, some intervals slightly flattened; apotypic, 16^{2-}, all intervals flat. Basis for designation: outgroup comparison.

Character 17. Male fore femur, ventral brush. Two states: plesiotypic, absent; apotypic, present (Figs. 7A-D). Basis for designation: outgroup comparison.

Character 18. Female, femora, setae on ventral surface. Four states: plesiotypic, absent; apotypic, on fore femur, only, 18^{a1}; apotypic , on fore and middle femur, 18^{a2}; and apotypic, setae absent, 18^{R-}, reversal, loss. Basis for designation: outgroup comparison and character correlation.

Character 19. Frons, surface sculpture. Two states: plesiotypic, smooth; apotypic, laterally longitudinally strigose. Basis for designation: outgroup comparison.

Character 20. Elytron, number of umbilical setae. Two states: plesiotypic, 14; apotypic, 16. Basis for designation: outgroup comparison.

Character 21. Left mandible, surface of retinacular groove. Two states: plesiotypic, smooth; apotypic, strigose. Basis for designation: outgroup comparison.

Character 22. Elytron, postero-lateral angles. Two states: plesiotypic, rounded; apotypic, spinose (Figs. 15A-E). Basis for designation: outgroup comparison.

Character 23. Pronotum, position of postero-lateral setae. Two states: plesiotypic, at postero-lateral angles; apotypic, anterad postero-lateral angles. Basis for designation: outgroup comparison.

Character 24. Relative size of head and pronotum. Two states: plesiotypic, HW/PW less than 1.0; apotypic, HW/PW more than 1.0. Basis for designation: outgroup comparison.

Character 25. Elytral interneurs, punctation. Three states: plesiotypic, impunctate; apotypic, punctate; apotypic, impunctate, 25^{R-}, reversal, loss. Basis for designation: outgroup comparison, and character correlation.

Character 26. Elytron, sutural angle. Two states: plesiotypic, not spinose; apotypic, spinose. Basis for designation: outgroup comparison.

Character 27. Width of molar area of mandibles. Two states: plesiotypic, relatively narrow (Figs. 27A-B); apotypic, relatively broad. Basis for designation: outgroup comparison.

Character 28. Elytra, color. This is a complex character, and is dealt with by species group, in part. Basis for designation is in part outgroup comparison and in part character correlation. Plesiotypic, bicolored, with preapical and premedial pale fasciae against a dark background (Fig. 14A and 15A-E); apotypic, general, elytra, unicolorous dark (28*), interpreted as increase of melanin deposition.

States of elytral color are designated separately for the *transversa* group (28t), *festiva* group (28f), and the *picea* + *aerata* complex (28p). For the *transversa* group, the pattern is: plesiotypic, bicolored, with black quite extensive (Fig. 20A); apotypic, five states, showing degrees of reduction of black pigment (Figs. 20H and I, 20G, 20B and C, 20E and 20D and F; $28t^{a1-}$, $^{a2-}$, $^{a3-}$, $^{a4-}$, and $^{a5-}$).

For the *festiva* group, five states are recognized: plesiotypic, pale fasciae quite extensive (Figs. 23B-C); apotypic, with dark color decreased, and pale fasciae enlarged, joined to one another or not , two states, $28f^{a1-}$, $^{a2-}$ (Figs. 23D-E) and apotypic, pale fasciae reduced, two states, $28f^{a1}$ and ^{a2} (Figs. 23A and H).

For the *picea* + *aerata* complex, unicolorous is postulated as plesiotypic (character correlation), with various reversals to the bicolored condition: apotypic, basal half of elytron pale, $28p^{a-}$ (Fig. 33E); apotypic, large pale preapical spot $28p^{b-}$ (Fig. 33D); and apotypic, large part of disc pale, lateral margins dark $28p^{c-}$ (Figs. 33A-C). Basis for designation: character correlation.

Character 29. Middle tibia of male, preapical notch. Two states: plesiotypic, absent; apotypic, present. Basis for designation: outgroup comparison.

Character 30. Left mandible, terebral groove. Two states: plesiotypic, smooth (Fig. 2E); apotypic, strigose (Fig. 4E). Basis for designation: character correlation.

Character 31. Pronotum, posterior margin. Four states: plesiotypic, straight (Fig. 7A); apotypic, convex, 31^{a1} (Fig. 7C); apotypic, lobed, 31^{a2} (Fig. 7B); apotypic, convex, 31^{a1R-}, a reversal. Basis for designation: character correlation.

Character 32. Right mandible, terebral groove. Two states: plesiotypic, smooth; apotypic, strigose. Basis for designation: character correlation.

Character 33. Abdominal sternum VII, males. Four states: plesiotypic, posterior margin even, not notched; apotypic 33^{a1}, shallowly notched; apotypic 33^{a2}, moderately to deeply notched;

apotypic 33^{R-}, not notched, reversal. Basis for designation: outgroup comparison, and reversal postulated on the basis of character correlation.

Character 34. Right mandible, posterior retinacular area. Three states: plesiotypic, smooth; apotypic, 34^{a1}, moderately strigose; apotypic, 34^{a2}, deeply and densely strigose (Fig. 4B). Basis for designation: character correlation.

Character 35. Mandible, molar groove. Two states: plesiotypic, broadly triangular (Fig. 2E); apotypic, more linear (Figs. 3E-F, K-L). Basis for designation: character correlation.

Character 36. Mandible, terebral strigils, length and extent. Three character states: plesiotypic, short, not extended to supraterebral ridge; apotypic, 36^{1}, short, extended to supraterebral ridge (Fig. 2A); apotypic, 36^{2}, long, extended to supraterebral ridge (Fig. 4G). Basis for designation: outgroup comparison and character correlation.

Character 37. Mandible, ventral groove. Three states: plesiotypic, longer (Figs. 2C-D); apotypic, 37^{a-}, shorter (Figs. 3C-D); apotypic, absent, 37^{b-}, loss (Figs. 3I-J). Basis for designation: outgroup comparison and character correlation.

Character 38. Male abdominal sternum III, setal patch. Three states: plesiotypic, absent; apotypic, present (Fig. 10A); apotypic 38^{R-}, absent, a loss and reversal. Basis for designation: outgroup comparison and character correlation.

Character 39. Male abdominal sternum IV, setal patch. Three states: plesiotypic, absent; apotypic, 39^{a1}, present, sparse (Fig.10A); apotypic, 39^{a2}, present, dense (Fig. 10B). Basis for designation: outgroup comparison.

Character 40. Elytron, lateral margin. Two states: plesiotypic, not explanate; apotypic, explanate. Basis for designation: outgroup comparison.

Character 41. Metasternum of male, setation. Three states: plesiotypic, glabrous; apotypic, 41^{a1}, sparsely setose (Fig. 10A); apotypic, 41^{a2}, densely setose. Basis for designation: outgroup comparison.

Character 42. Head, color. Three states: plesiotypic, dark; apotypic, 42^{1-} apotypic, 42^{2-}, pale; interpreted as a loss of melanin. Basis for designation: character correlation.

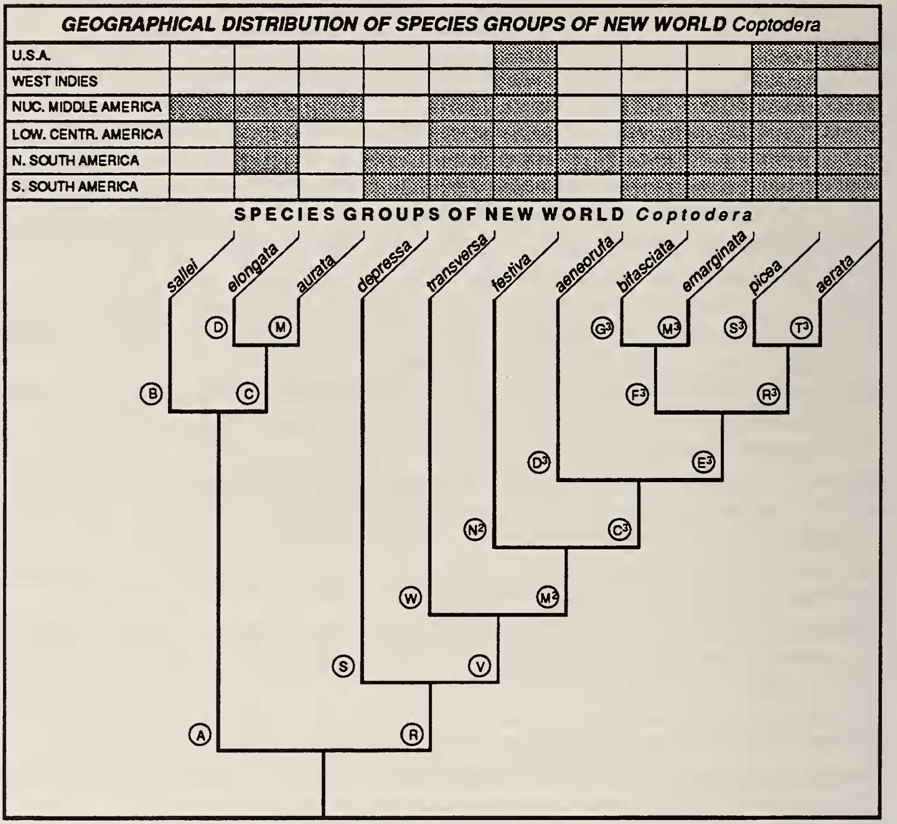
Character 43. Pronotum, color. Two states: plesiotypic, dark; apotypic, 43^{-} pale, interpreted as a result of depigmentation. Basis for designation: character correlation.

Character 44. Fore tibia, upper spur. Three states: plesiotypic, normally developed (Fig. 9A); apotypic, 44^{1-}, shortened slightly (Figs. 9C-D); apotypic, 44^{2-}, reduced to a small stub (Figs. 9F-G). Basis for designation: outgroup comparison.

Character 45. Pronotum, color. Three states: plesiotypic, unicolorous; apotypic, bicolored to pale; apotypic 45^{R-} unicolorous, interpreted as a reversal. Basis for designation: outgroup comparison and character correlation.

Characters 46, 47, and 48. Male genitalia, internal sac, macrospines. The variation pattern is complex, and postulated homoplasy is substantial. For designation of character states, macrospines were postulated as ancestral for lineage C^3 (character 11^b). Further, three groups are postulated as ancestral (A, B, and C), and the macrospines of each spine group are postulated to have been of moderate size (*i.e.*, intermediate), with apotypic variants smaller or larger. Absence of a macrospine group is postulated to be a loss.

The basis for these postulates is as follows. All of the spine groups are present in most of the species in each of the species groups that comprise lineage M^2 (Figs. 35 and 36). Thus it seems parsimonious to infer that such would be true of the ancestral stock of lineage M^2, as well. A corollary is that absence of a spine group within lineage M^2 is the result of loss. Using moderate size as plesiotypic is based on a further postulate that ancestrally all spine groups were close to one another in size, with each group originating from similar precursors.



GEOGRAPHICAL DISTRIBUTION OF SPECIES GROUPS OF NEW WORLD *Coptodera*

	sallei	elongata	aurata	depressa	transversa	festiva	aeneorufa	bifasciata	emarginata	picea	aerata
U.S.A.						▨				▨	▨
WEST INDIES						▨				▨	
NUC. MIDDLE AMERICA	▨	▨	▨		▨	▨		▨	▨	▨	▨
LOW. CENTR. AMERICA		▨			▨	▨		▨	▨	▨	▨
N. SOUTH AMERICA		▨		▨	▨	▨	▨	▨	▨	▨	▨
S. SOUTH AMERICA				▨	▨	▨		▨	▨	▨	▨

FIGURE 35. Reconstructed phylogeny of the New World species groups of the genus *Coptodera* Dejean, and their geographical distribution, in terms of major zoogeographic areas. Encircled capital letters are designations for lineages.

Character 46. Macrospine group A. Six states: plesiotypic, moderate size (Figs. 25A-B); apotypic, large, 46^1 (Figs. 28E-F and 34A-B); apotypic, very large 46^2 (Figs. 27A-H); apotypic, smaller, 46^{1-} (Figs. 34C-D); apotypic, very small, 46^{2-} (Figs. 34E-H); apotypic, absent, 46^{R-} (Figs. 24I-J and 28C-D), interpreted as a loss and reversal.

Character 47. Macrospine group B. Ten states: plesiotypic, size moderate, two spines (Figs. 24C-D, 27C-D, and 32A-B); apotypic, two spines, size progressively larger, 47^1 (Figs. 24K-L), 47^2 (Figs. 24O-P); size moderate, three spines, 47^x (Figs. 25A-B); apotypic, size progressively smaller, 47^{1-} (Figs. 28C-D), 47^{2-} (Figs. 34E-F), and 47^{3-} (Figs. 34G-H); apotypic, size moderate, one spine, 47^{R1-} (Figs. 24G-H and 27A-B); and macrospine group B absent, 47^{R2-} (Figs. 24A-B) interpreted as a reversal and loss. The basis for postulating two as plesiotypic for macrospine group B is that this is the more common than, and at least as widespread as, the other numbers combined.

Character 48. Macrospine group C. Seven states: plesiotypic, size moderate, two spines (Figs. 27C-F; apotypic, size progressively larger, 48^{1} (Figs. 24A-B), and 48^{2} (Figs. 29I-J, 29K-L); apotypic, size progressively smaller, two spines, 48^{1-} (Figs. 27A-B), and 48^{2-} (Figs. 34E-F); size moderate, one spine, 48^{R1-} (Figs. 25A-B); and macrospine group C absent, 48^{R2-} (Figs. 32A-B). See explanation under macrospine group C above, for designation of spine number.

Character 49. Median lobe, form of ventral surface. Two states: plesiotypic, curved; apotypic, straight (Figs. 24C, E, M and O). Basis for designation: character correlation.

Character 50. Tarsal claws, pectination, size of pectens. Three states: plesiotypic, size moderate, extended over much of ventral surface of claw (Fig. 9E); apotypic, pectens enlarged (Fig. 8H); apotypic, 48^{-}, pectens reduced, restricted to basal area of each claw (Fig. 9B). Basis for designation: the state postulated as plesiotypic is the most widespread, being represented in all species groups of *Coptodera*. The same result would be obtained by character correlation or functional outgroup-ingroup comparison.

Character 51. Mandible, relative length of terebra. Three states: plesiotypic, elongate (Figs. 2A-B, 3A-B, and 3G-H); apotypic, 51^{1-}, reduced moderately (Figs. 4G-H); apotypic, 51^{2-}, reduced markedly (Figs. 4A-B). Basis for designation: character correlation.

Character 52. Male, mid tarsus, adhesive vestiture. Two states: plesiotypic, absent; apotypic, present. Basis for designation: outgroup comparison.

Character 53. Elytron, apical margin near suture. Two states: plesiotypic, straight; apotypic, sinuate. Basis for designation: outgroup comparison.

Character 54. Clypeus and frons, surface. Two states: plesiotypic, glabrous; apotypic, setose. Basis for designation: character correlation.

Character 55. Antennomeres 5-11, sensory pits. Two states: plesiotypic, absent; apotypic, present. Basis for designation: outgroup comparison and character correlation.

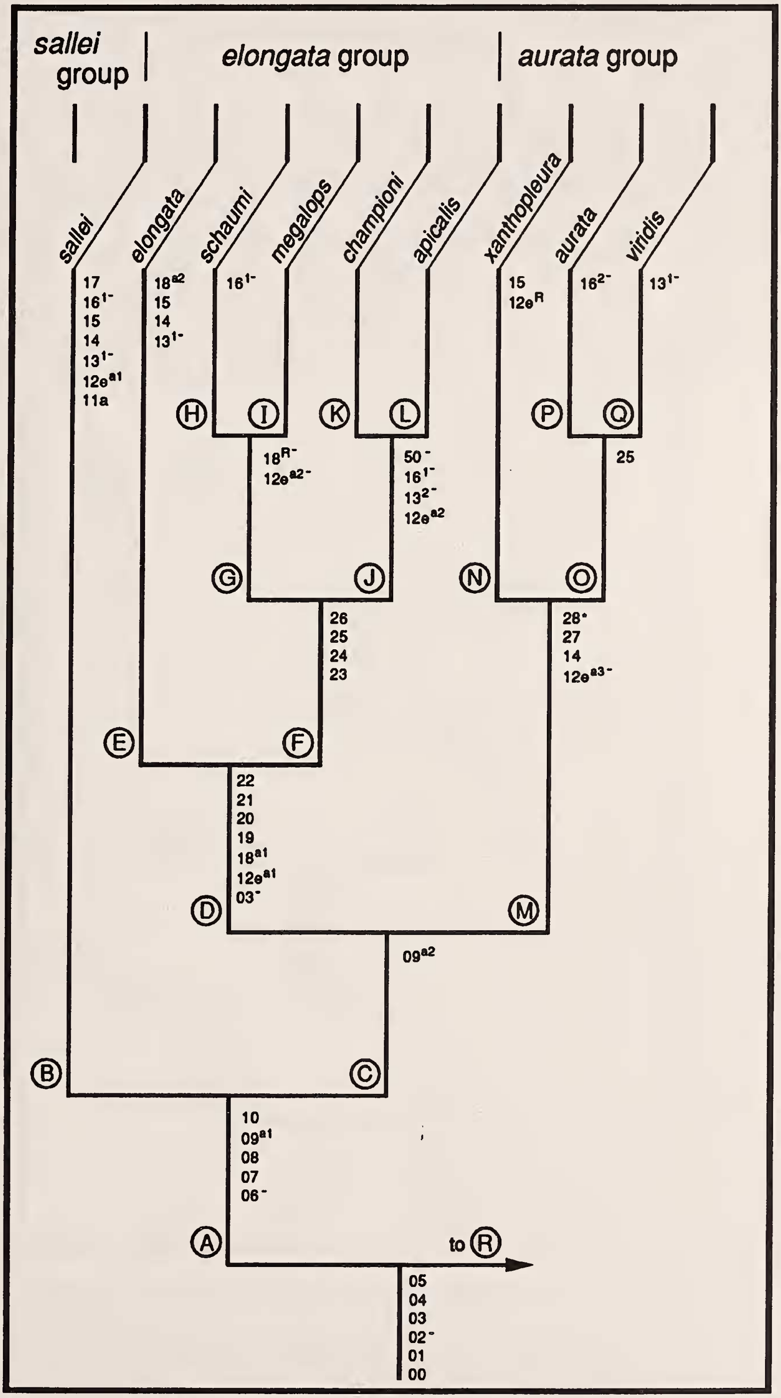
Character 56. Vertex of head, surface. Two states: plesiotypic, glabrous; apotypic, setose. Basis for designation: outgroup comparison and character correlation.

Evolution of structural features

An evolutionary analysis of a taxon seeks correlations of holomorphological patterns with habitat occupied and with way of life. Such correlation permits postulation of the details of the holomorphological features as adaptations to the environment, or the partial fitting of species to the "habitat template" (Southwood 1987). For *Coptodera*, although the general pattern of way of life has been identified (see above), the details are not known that would permit access to the holistic and highly enlightening "habitat template approach" of adaptational analysis (Spence 1989: 2445-2446). Instead, attention is drawn to the cladistic patterns postulated (*cf.* Figs. 35 and 36), with the expectation that such focus will facilitate discovery of the information needed for a more integrated and informative synthesis. Following is a series of comments, based on the reconstructed phylogeny presented in Fig. 36, intended to focus attention on the characters and their states as parts of adaptive complexes rather than as symbols for manipulation in a cladistic context.

General features.-- Table XIII shows that of 136 character states presented in the phylogenetic analysis, approximately one third arose more than once—from two to nine times. Some of these convergences are postulated reversals. Character states evolving the most frequently (nine times

FIGURE 36. Reconstructed phylogeny of the New World species of the genus *Coptodera* Dejean: *C. sallei*, *C. elongata* and *C. aurata* groups. Encircled capital letters are designations for lineages. Numbers and associated lower-case letters designate apotypic character states. See Table XII and text for details.


sallei group
elongata group
aurata group
sallei
elongata
schaumi
megalops
championi
apicalis
xanthopleura
aurata
viridis
17 16^{1-} 15 14 13^{1-} $12e^{a1}$ 11a
18^{a2} 15 14 13^{1-}
16^{1-}
15 $12e^{R}$
16^{2-}
13^{1-}
H
I
K
L
P
Q
18^{R-} $12e^{a2-}$
50^{-} 16^{1-} 13^{2-} $12e^{a2}$
25
G
J
N
O
26 25 24 23
28^{*} 27 14 $12e^{a3-}$
E
F
22 21 20 19 18^{a1} $12e^{a1}$ 03^{-}
D
M
09^{a2}
B
C
10 09^{a1} 08 07 06^{-}
A
to R
05 04 03 02^{-} 01 00

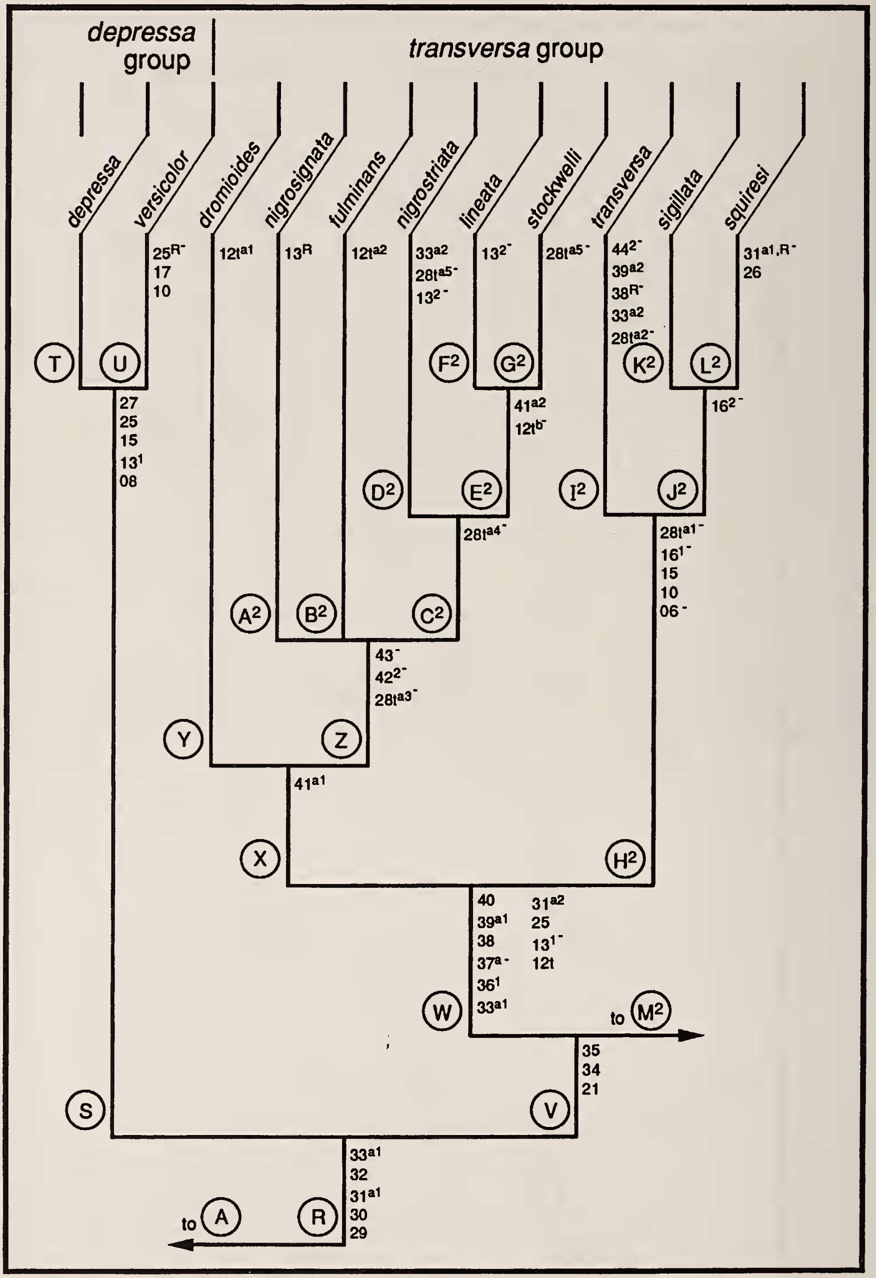


FIGURE 36 - continued. *Coptodera depressa* and *C. transversa* groups.

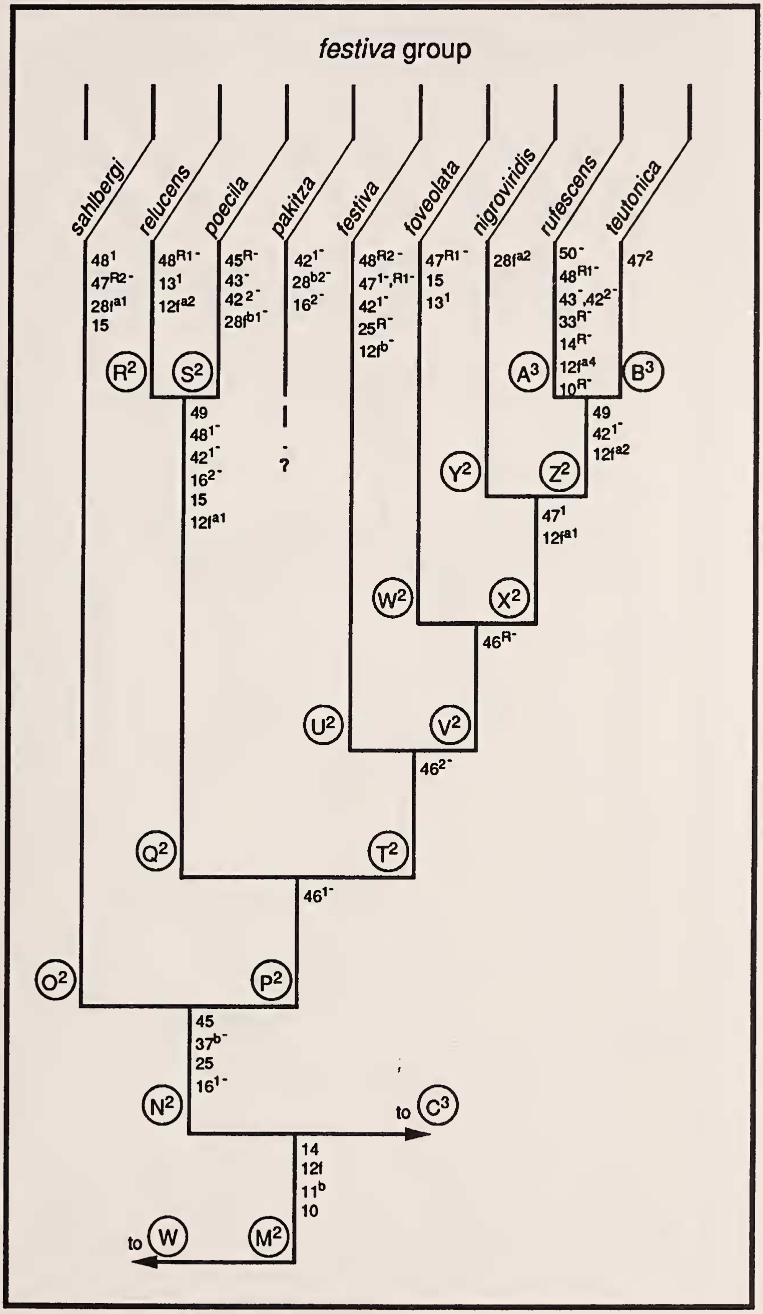


FIGURE 36 - continued. *Coptodera festiva* group.

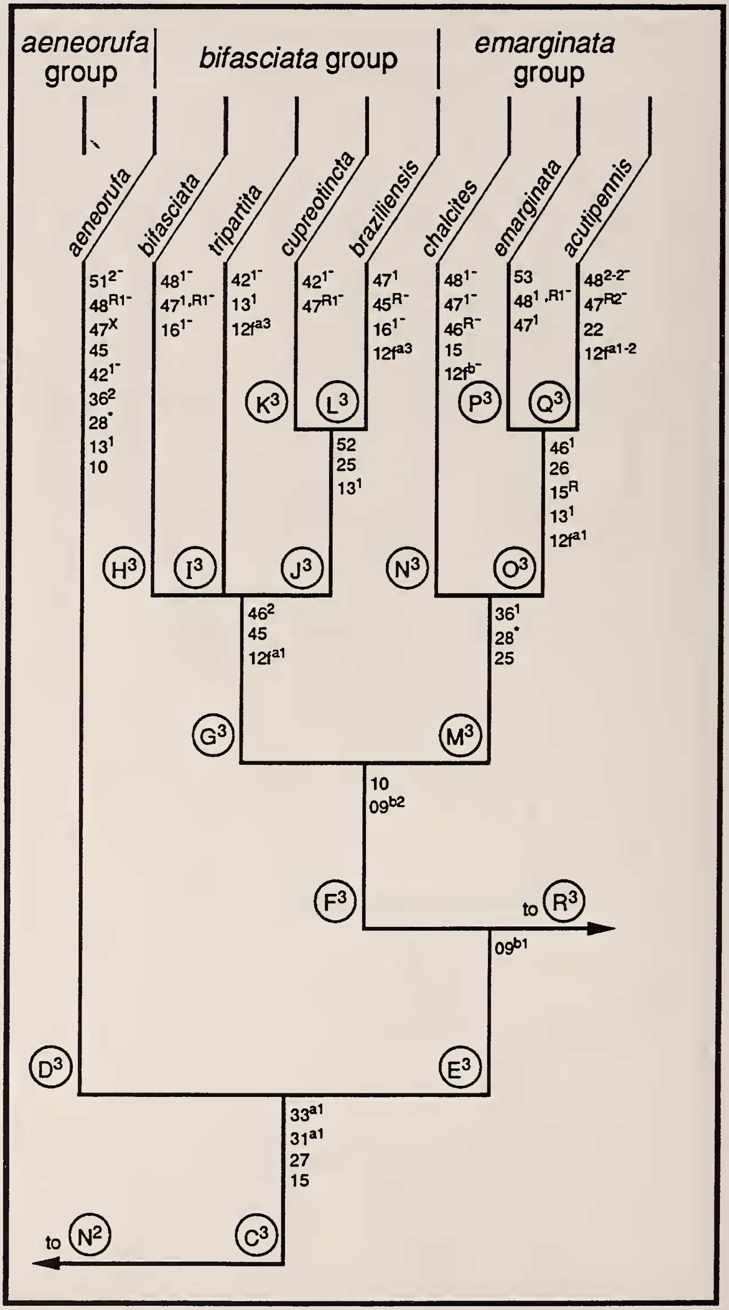

aeneorufa group
bifasciata group
emarginata group
aeneorufa
bifasciata
tripartita
cupreotincta
braziliensis
chalcites
emarginata
acutipennis
51^{2-} 48^{R1-} 47^{X} 45 42^{1-} 36^{2} 28^{*} 13^{1} 10
48^{1-} $47^{1,R1-}$ 16^{1-}
42^{1-} 13^{1} $12f^{a3}$
42^{1-} 47^{R1-}
47^{1} 45^{R-} 16^{1-} $12f^{a3}$
48^{1-} 47^{1-} 46^{R-} 15 $12f^{b-}$
53 $48^{1,R1-}$ 47^{1}
48^{2-2-} 47^{R2-} 22 $12f^{a1-2}$
K3
L3
P3
Q3
52 25 13^{1}
46^{1} 26 15^{R} 13^{1} $12f^{a1}$
H3
I3
J3
N3
O3
46^{2} 45 $12f^{a1}$
36^{1} 28^{*} 25
G3
M3
10 09^{b2}
F3
to R3
09^{b1}
D3
E3
33^{a1} 31^{a1} 27 15
to N2
C3

FIGURE 36 - continued. *Coptodera aeneorufa*, *C. bifasciata* and *C. emarginata* groups.

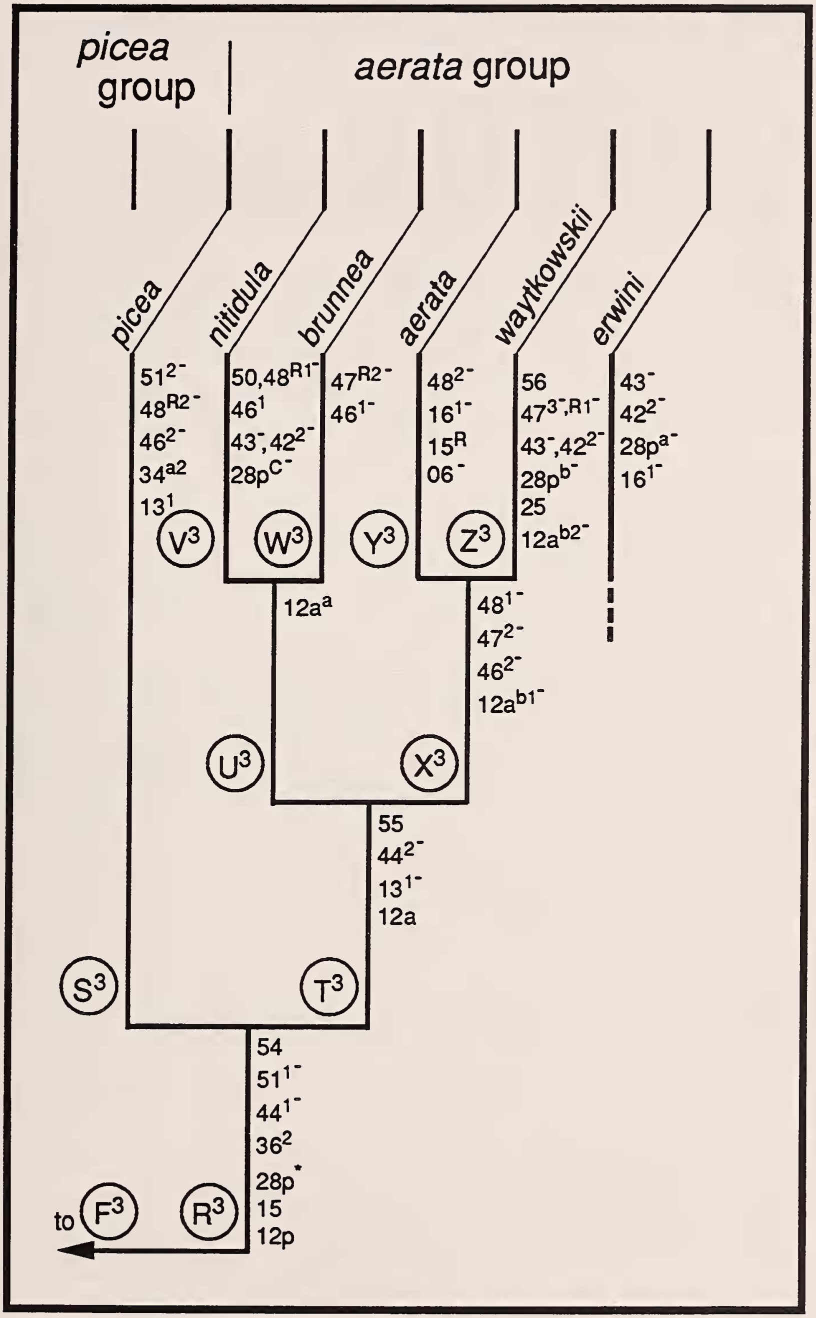


FIGURE 36 - continued. *Coptodera picea* and *C. aerata* groups.

TABLE XII. Characters and distributions of phylogenetically designated character states among the New World species of the genus *Coptodera* Dejean. See text for explanation of details.

	CHARACTERS AND CHARACTER STATES														
SPECIES	**00**	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**
sallei	x	x	x^-	x	x	x	x^-	x	x	x^{a1}	x	x^{a}	xe^{a1}	x^{1-}	x
elongata	x	x	x^-	x^-	x	x	x^-	x	x	x^{a2}	x	—	xe^{a1}	x^{1-}	x
schaumi	x	x	x^-	x^-	x	x	x^-	x	x	x^{a2}	x	—	xe^{a2-}	—	—
megalops	x	x	x^-	x^-	x	x	x^-	x	x	x^{a2}	x	—	xe^{a2-}	—	—
championi	x	x	x^-	x^-	x	x	x^-	x	x	x^{a2}	x	—	xe^{a2}	x^{2-}	—
apicalis	x	x	x^-	x^-	x	x	x^-	x	x	x^{a2}	x	—	xe^{a2}	x^{2-}	—
xanthopleura	x	x	x^-	x	x	x	x^-	x	x	x^{a2}	x	—	$xe^{a3-,R}$	—	x
aurata	x	x	x^-	x	x	x	x^-	x	x	x^{a2}	x	—	xe^{a3-}	—	x
viridis	x	x	x^-	x	x	x	x^-	x	x	x^{a2}	x	—	xe^{a3-}	x^{1-}	x
depressa	x	x	x^-	x	x	x	—	—	x	—	—	—	—	x^{1}	—
versicolor	x	x	x^-	x	x	x	—	—	x	—	x	—	—	x^{1}	—
dromioides	x	x	x^-	x	x	x	—	—	—	—	—	—	xt^{a1}	x^{1-}	—
nigrosignata	x	x	x^-	x	x	x	—	—	—	—	—	—	xt	x^{R}	—
fulminans	x	x	x^-	x	x	x	—	—	—	—	—	—	xt^{a2}	x^{1-}	—
nigrostriata	x	x	x^-	x	x	x	—	—	—	—	—	—	xt	x^{2-}	—
lineata	x	x	x^-	x	x	x	—	—	—	—	—	—	xt^{b-}	x^{2-}	—
stockwelli	x	x	x^-	x	x	x	—	—	—	—	—	—	xt^{b-}	x^{1-}	—
transversa	x	x	x^-	x	x	x	x^-	—	—	—	x	—	xt	x^{1-}	—
sigillata	x	x	x^-	x	x	x	x^-	—	—	—	x	—	xt	x^{1-}	—
squiresi	x	x	x^-	x	x	x	x^-	—	—	?	x	?	?	?	—
sahlbergi	x	x	x^-	x	x	x	—	—	—	—	x	x^{b}	xf	—	x
relucens	x	x	x^-	x	x	x	—	—	—	—	x	x^{b}	xf^{a2}	x^{1}	x
poecila	x	x	x^-	x	x	x	—	—	—	—	x	x^{b}	xf^{a1}	—	x
pakitza	x	x	x^-	x	x	x	—	—	—	?	x	?	?	?	x
festiva	x	x	x^-	x	x	x	—	—	—	—	x	x^{b}	xf^{b-}	—	x
foveolata	x	x	x^-	x	x	x	—	—	—	—	x	x^{b}	xf	x^{1}	x
nigroviridis	x	x	x^-	x	x	x	—	—	—	—	x	x^{b}	xf^{a1}	—	x
rufescens	x	x	x^-	x	x	x	—	—	—	—	x^{R-}	x^{b}	xf^{a4}	—	x^{R-}
teutonica	x	x	x^-	x	x	x	—	—	—	—	x	x^{b}	xf^{a2}	—	x
aeneorufa	x	x	x^-	x	x	x	—	—	—	—	x	x^{b}	—	x^{1}	x
bifasciata	x	x	x^-	x	x	x	—	—	—	x^{b2}	x	x^{b}	xf^{a1}	—	x
tripartita	x	x	x^-	x	x	x	—	—	—	x^{b2}	x	x^{b}	xf^{a3}	x^{1-}	x
cupreotincta	x	x	x^-	x	x	x	—	—	—	x^{b2}	x	x^{b}	xf^{a1}	x^{1}	x
braziliensis	x	x	x^-	x	x	x	—	—	—	x^{b2}	x	x^{b}	xf^{a3}	x^{1}	x
chalcites	x	x	x^-	x	x	x	—	—	—	x^{b2}	x	x^{b}	xf^{b-}	—	x
emarginata	x	x		x	x	x	—	—	—	x^{b2}	x	x^{b}	xf^{a1}	x^{1}	x
acutipennis	x	x	x^-	x	x	x	—	—	—	x^{b2}	x	x^{b}	xf^{a1}	x^{1}	x
picea	x	x	x^-	x	x	x	—	—	—	x^{b1}	x	x^{b}	xp	x^{1}	x
nitidula	x	x	x^-	x	x	x	—	—	—	x^{b1}	x	x^{b}	xa^{a}	x^{1-}	x
brunnea	x	x	x^-	x	x	x	—	—	—	x^{b1}	x	x^{b}	xa^{a}	x^{1-}	x
aerata	x	x	x^-	x	x	x	x^-	—	—	x^{b1}	x	x^{b}	xa^{b1-}	x^{1-}	x
waytkowskii	x	x	x^-	x	x	x	—	—	—	x^{b1}	x	x^{b}	xa^{b2-}	x^{1-}	x
erwini	x	x	x^-	x	x	x	—	—	—	?	x	?	?	?	x

LEGEND : —— plesiotypic, x apotypic, ? absent data

TABLE XII - continued - 2.

	CHARACTERS AND CHARACTER STATES													
SPECIES	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**
sallei	x	x^{1-}	x	—	—	—	—	—	—	—	—	—	—	—
elongata	x	—	—	x^{a2}	x	x	x	x	—	—	—	—	—	—
schaumi	—	x^{1-}	—	x^{R-}	x	x	x	x	x	x	x	x	—	—
megalops	—	—	—	x^{R-}	x	x	x	x	x	x	x	x	—	—
championi	—	x^{1-}	—	x^{a1}	x	x	x	x	x	x	x	x	—	—
apicalis	—	x^{1-}	—	x^{a1}	x	x	x	x	x	x	x	x	—	—
xanthopleura	x	—	—	—	—	—	—	—	—	—	—	—	x	x^{*}
aurata	—	x^{2-}	—	—	—	—	—	—	—	—	x	—	x	x^{*}
viridis	—	—	—	—	—	—	—	—	—	—	x	—	x	x^{*}
depressa	x	—	—	—	—	—	—	—	—	—	x	—	x	—
versicolor	x	—	x	—	—	—	—	—	—	—	x^{R-}	—	x	—
dromioides	—	—	—	—	—	—	x	—	—	—	x	—	—	—
nigrosignata	—	—	—	—	—	—	x	—	—	—	x	—	—	xt^{a3-}
fulminans	—	—	—	—	—	—	x	—	—	—	x	—	—	xt^{a3-}
nigrostriata	—	—	—	—	—	—	x	—	—	—	x	—	—	xt^{a5-}
lineata	—	—	—	—	—	—	x	—	—	—	x	—	—	xt^{a4-}
stockwelli	—	—	—	—	—	—	x	—	—	—	x	—	—	xt^{a5-}
transversa	x	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	xt^{a2-}
sigillata	x	x^{2-}	—	—	—	—	x	—	—	—	x	—	—	xt^{a1-}
squiresi	x	x^{2-}	—	—	—	—	x	—	—	—	x	x	—	xt^{a1-}
sahlbergi	x	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	xf^{a1}
relucens	x	x^{2-}	—	—	—	—	x	—	—	—	x	—	—	—
poecila	x	x^{2-}	—	—	—	—	x	—	—	—	x	—	—	xf^{b1-}
pakitza	—	x^{2-}	—	—	—	—	x	—	—	—	x	—	—	xf^{b2-}
festiva	—	x^{1-}	—	—	—	—	x	—	—	—	x^{R-}	—	—	—
foveolata	x	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	—
nigroviridis	—	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	xf^{a2}
rufescens	—	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	—
teutonica	—	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	—
aeneorufa	x	—	—	—	—	—	x	—	—	—	—	—	x	x^{*}
bifasciata	x	x^{1-}	—	—	—	—	x	—	—	—	—	—	x	—
tripartita	x	—	—	—	—	—	x	—	—	—	—	—	x	—
cupreotincta	x	—	—	—	—	—	x	—	—	—	x	—	x	—
braziliensis	x	x^{1-}	—	—	—	—	x	—	—	—	x	—	x	—
chalcites	x	—	—	—	—	—	x	—	—	—	x	—	x	x^{*}
emarginata	x^{R}	—	—	—	—	—	x	—	—	—	x	x	x	x^{*}
acutipennis	x^{R}	—	—	—	—	—	x	—	—	—	x	x	x	x^{*}
picea	x	—	—	—	—	—	x	—	—	—	—	—	x	xp^{*}
nitidula	x	—	—	—	—	—	x	—	—	—	—	—	x	xp^{c-}
brunnea	x	—	—	—	—	—	x	—	—	—	—	—	x	xp
aerata	x^{R}	x^{1-}	—	—	—	—	x	—	—	—	—	—	x	xp
waytkowskii	x	—	—	—	—	—	x	—	—	—	x	—	x	xp^{b-}
erwini	x	x^{1-}	—	—	—	—	x	—	—	—	—	—	x	xp^{a-}

LEGEND : —— plesiotypic, x apotypic, ? absent data

TABLE XII - continued - 3.

	CHARACTERS AND CHARACTER STATES													
SPECIES	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**
sallei	—	—	—	—	—	—	—	—	—	—	—	—	—	—
elongata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
schaumi	—	—	—	—	—	—	—	—	—	—	—	—	—	—
megalops	—	—	—	—	—	—	—	—	—	—	—	—	—	—
championi	—	—	—	—	—	—	—	—	—	—	—	—	—	—
apicalis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
xanthopleura	—	—	—	—	—	—	—	—	—	—	—	—	—	—
aurata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
viridis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
depressa	x	x	x^{a1}	x	x^{a1}	—	—	—	—	—	—	—	—	—
versicolor	x	x	x^{a1}	x	x^{a1}	—	—	—	—	—	—	—	—	—
dromioides	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a1}	—
nigrosignata	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a1}	x^{2-}
fulminans	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a1}	x^{2-}
nigrostriata	x	x	x^{a2}	x	x^{a2}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a1}	x^{2-}
lineata	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a2}	x^{2-}
stockwelli	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a2}	x^{2-}
transversa	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x^{R-}	x^{a2}	x	—	—
sigillata	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	—	—
squiresi	x	x	x^{a1R-}	x	?	x^{a1}	x	x^{1}	x^{a-}	?	?	x	—	—
sahlbergi	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	—
relucens	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	x^{1-}
poecila	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	x^{2-}
pakitza	x	x	x^{a1}	x	?	x^{a1}	x	—	x^{b-}	?	?	—	—	x^{1-}
festiva	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	x^{1-}
foveolata	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	—
nigroviridis	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	—
rufescens	x	x	x^{a1}	x	x^{R-}	x^{a1}	x	—	x^{b-}	—	—	—	—	x^{2-}
teutonica	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	x^{1-}
aeneorufa	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{2}	—	—	—	—	—	x^{1-}
bifasciata	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	—	—	—	—	—	—
tripartita	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	—	—	—	—	—	x^{1-}
cupreotincta	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	—	—	—	—	—	x^{1-}
braziliensis	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	—	—	—	—	—	—
chalcites	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{1}	—	—	—	—	—	—
emarginata	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{1}	—	—	—	—	—	—
acutipennis	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{1}	—	—	—	—	—	—
picea	x	x	x^{a1}	x	x^{a1}	x^{a2}	x	x^{2}	—	—	—	—	—	—
nitidula	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{2}	—	—	—	—	—	x^{2-}
brunnea	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{2}	—	—	—	—	—	—
aerata	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{2}	—	—	—	—	—	—
waytkowskii	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{2}	—	—	—	—	—	x^{2-}
erwini	x	x	x^{a1}	x	?	x^{a1}	x	x^{2}	—	?	?	—	—	x^{2-}

LEGEND : — plesiotypic, x apotypic, ? absent data

TABLE XII - continued - 4.

	CHARACTERS AND CHARACTER STATES													
SPECIES	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**
sallei	—	—	—	—	—	—	—	—	—	—	—	—	—	—
elongata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
schaumi	—	—	—	—	—	—	—	—	—	—	—	—	—	—
megalops	—	—	—	—	—	—	—	—	—	—	—	—	—	—
championi	—	—	—	—	—	—	—	x^{-}	—	—	—	—	—	—
apicalis	—	—	—	—	—	—	—	x^{-}	—	—	—	—	—	—
xanthopleura	—	—	—	—	—	—	—	—	—	—	—	—	—	—
aurata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
viridis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
depressa	—	—	—	—	—	—	—	—	—	—	—	—	—	—
versicolor	—	—	—	—	—	—	—	—	—	—	—	—	—	—
dromioides	—	—	—	—	—	—	—	—	—	—	—	—	—	—
nigrosignata	x^{-}	—	—	—	—	—	—	—	—	—	—	—	—	—
fulminans	x^{-}	—	—	—	—	—	—	—	—	—	—	—	—	—
nigrostriata	x^{-}	—	—	—	—	—	—	—	—	—	—	—	—	—
lineata	x^{-}	—	—	—	—	—	—	—	—	—	—	—	—	—
stockwelli	x^{-}	—	—	—	—	—	—	—	—	—	—	—	—	—
transversa	—	x^{2-}	—	—	—	—	—	—	—	—	—	—	—	—
sigillata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
squiresi	—	—	—	?	?	?	?	—	—	—	—	—	—	—
sahlbergi	—	—	x	—	x^{R2-}	x^{1}	—	—	—	—	—	—	—	—
relucens	—	—	x	x^{1-}	—	x^{R1-}	x	—	—	—	—	—	—	—
poecila	x^{-}	—	x^{R-}	x^{1-}	—	x^{1-}	x	—	—	—	—	—	—	—
pakitza	—	—	x	?	?	?	?	—	—	—	—	—	—	—
festiva	—	—	x	x^{2-}	$x^{1;R1-}$	x^{R2-}	—	—	—	—	—	—	—	—
foveolata	—	—	x	x^{R-}	x^{R1-}	—	—	—	—	—	—	—	—	—
nigroviridis	—	—	x	x^{R-}	x^{1}	—	—	—	—	—	—	—	—	—
rufescens	x^{-}	—	x	x^{R-}	x^{1}	x^{R1-}	x	x^{-}	—	—	—	—	—	—
teutonica	—	—	x	x^{R-}	x^{2}	—	x	—	—	—	—	—	—	—
aeneorufa	—	—	x	—	x^{x}	x^{R1-}	—	—	x^{2-}	—	—	—	—	—
bifasciata	—	—	x	x^{2}	$x^{1,R1-}$	x^{1-}	—	—	—	—	—	—	—	—
tripartita	—	—	x	x^{2}	—	—	—	—	—	—	—	—	—	—
cupreotincta	—	—	x	x^{2}	x^{R1-}	—	—	—	—	x	—	—	—	—
braziliensis	—	—	x	x^{2}	x^{1}	—	—	—	—	x	—	—	—	—
chalcites	—	—	—	x^{R-}	x^{1-}	x^{1-}	—	—	—	—	—	—	—	—
emarginata	—	—	—	x^{1}	x^{1}	$x^{1;R1-}$	—	—	x^{2-}	—	x	—	—	—
acutipennis	—	—	—	x^{1-b2-}	x^{R2-}	x^{2-2-}	—	—	—	—	—	—	—	—
picea	—	x^{1-}	—	x^{2-}	—	x^{R2-}	—	—	x^{2-}	—	—	x	—	—
nitidula	x^{-}	x^{2-}	—	x^{1}	—	x^{R1-}	—	x	x^{1-}	—	—	x	x	—
brunnea	—	x^{2-}	—	x^{1-}	x^{R2-}	—	—	—	x^{1-}	—	—	x	x	—
aerata	—	x^{2-}	—	x^{2-}	x^{2-}	x^{2-}	—	—	x^{1-}	—	—	x	x	—
waytkowskii	x^{-}	x^{2-}	—	x^{2-}	x^{3-}	x^{1-}	—	—	x^{1-}	—	—	x	x	x
erwini	x^{-}	x^{2-}	—	?	?	?	?	—	x^{1-}	—	—	x	x	—

LEGEND : — plesiotypic, x apotypic, ? absent data

TABLE XIII. Frequency of appearance of apotypic character states among the New World species of *Coptodera* Dejean.

No. of Character States	No. of Independent Appearances
84	1
22	2
13	3
4	4
2	5
7	6
1	7
1	8
2	9
Total 136	

each) are transverse microsculpture of the elytra (character 15) and slight flattening of the elytral intervals (character 16^{1-}). Punctation of elytral intervals (character 25) evolved eight times.

Character 13, which evolved seven times, involves the membranous portion of the median lobe. The significance of such a change is not evident.

Character reversals.-- Apparent plesiotypic states are postulated to have arisen from apotypic states a total of 27 times, in 14 characters. For overall appearance, a dull dorsal surface has evolved from a shiny surface once (*C. xanthopleura*); isodiametric microsculpture of the elytra has evolved from the transverse patterns twice (in *C. emarginata* and *C. aerata*). Reversals in color pattern have occurred: for the pronotum, unicolorous has evolved from bicolored (*C. poecila*); and for the elytra, bicolored has evolved from unicolorous three times (in *C. nitidula*, *C. waytkowskii*, and *C. erwini*). The basal lobe of the pronotum has been reduced once (in *C. squiresi*).

For setation, a patch of setae on the ventral surface of the fore femora of females, a postulated synapotypy of the *elongata* group (lineage D), is postulated to have been lost once in lineage G (*C. schaumi* and *C. megalops*).

Fourteen reversals and reductions in number of parts have occurred in the macrospine complement of the male genitalia: macrospine A has been lost twice (once in lineage V^2, the *C. foveolata-nigroviridis-rufescens-teutonica* lineage; and once in *C. chalcites*); macrospine group B has been reduced to a single spine four times (*C. festiva*, *foveolata*, *bifasciata*, and *cupreotincta*), and lost once (in *C. sahlbergi*); macrospine group C has been reduced to a single spine five times (in *C. relucens*, *foveolata*, *aeneorufa*, *emarginata*, and *nitidula*), and lost twice (in *C. festiva* and *C. picea*).

These rather numerous reversals suggest that the genetic bases of these structural features are rather simple, and that direction of selection is not sustained.

Body size.-- This feature was not used in reconstructing the phylogeny of *Coptodera*. Nonetheless, size is an important characteristic of evolution of taxa, and so it is included as an aspect of the evolutionary analysis. Figure 37 illustrates for species groups the range of body size in mm., and mid-point of the range, in terms of Standardized Body Length. Most species groups, including the less derived lineages (descendants of lineage A, Fig. 35), and the basal *depressa* group of the more derived lineage R, are represented in the range 5.5-7.5 mm. Accordingly, we accept this range as ancestral.

Evolution of body size, then, has been in two directions: reduction and increase. Size has decreased in the *transversa* group (lineage W) and in lineage R^3, including the *picea* and *aerata* species groups. These two assemblages are not closely related, and so body size must have been reduced twice. Also, larger size has evolved independently three times: in the *C. elongata*, *festiva*, and *emarginata* groups.

No overall phyletic pattern in size variation is evident. Liebherr (1988: 158) summarizes the biological significance of increased and decreased body size. The significance of such changes in *Coptodera* are not known.

Body form.-- Explanation of the elytra (character 40) evolved in the *transversa* group (lineage W). This change is correlated with a more variegated color pattern and overall paler color.

A different change in body form involves relative head size (character 24), which evolved in lineage F, of the *elongata* group. The members of this lineage resemble members of the genus *Pericalus* Macleay, the adelphotaxon of *Coptodera*. Probably this change has to do with improved vision posteriorly, or vision all around.

Explanation of the pronotum evolved in four lineages (B, E, M, and M^2), with a reversal in *C. rufescens*, a member of lineage M^2. This change seems not to be correlated with other changes in body form.

Appearance of the dorsal surface.-- The following comments focus on the elytra because these sclerites comprise most of the dorsal surface, and exhibit for this area most of the features that were used in the phylogenetic analysis. A dull surface (character 10) is postulated to be plesiotypic for the New World species of *Coptodera*, even though this state is confined to adults of the *C. depressa* (lineage S) and *transversa* (lineage X) species groups. A shining or lustrous surface is correlated with metallic color and less precisely with transverse microsculpture (character 15). Also correlated with a lustrous surface is smoothness, meaning for *Coptodera* adults with more or less flattened elytral intervals (character 16).

Ball and Shpeley (1983: 800) suggest that the glint from a lustrous surface can "confuse a predator about the exact position of its prey, thus giving the latter an enhanced probability of escape". Erwin (1979b: 547-548) notes that a lustrous surface ("metallic coloration") is correlated with individuals that are surface-active in searching for food and mates. As recorded above, most species of *Coptodera* seem to be surface-active, on tree trunks and branches, or on the ground, at night, including species of the *transversa* group that exhibit a dull surface. Thus, a simple ecological correlate with lustrousness is elusive. Nonetheless, if our postulate is correct that a lustrous surface is derived, then strong selection is favoring development and maintenance of such a condition, an inference based on the numerous times postulated for its development and the generally parallel development of transverse microsculpture.

Punctation of the elytral interneurs (character 25) must influence appearance of the dorsal surface also, but we do not know what the influence might be. We note that, because of its frequent derivation in *Coptodera*, selection for punctate interneurs must be marked.

Color pattern of the dorsal surface.-- Color was analyzed as four characters: head (dark or pale, character 42); pronotum (dark or pale, character 43; and unicolorous or bicolored, character 45); and elytra (dark, bicolored with pale fasciae; and pale, bicolored with dark fasciae, character 28). The postulated ancestral pattern is: head and pronotum uniformly dark, and elytra bicolored—two pale fasciae on a dark background.

Fig. 38 is a diagram representing our concept of evolution of color pattern. Organized hierarchically, three groups of derived patterns are recognized: 1, dorsal surface unicolorous (1A; subsequently, depigmentation occurred, as noted below); 2, elytra bicolored, with dark fasciae against a pale background (2A and 2B); and 3, pronotum bicolored, and elytra bicolored with

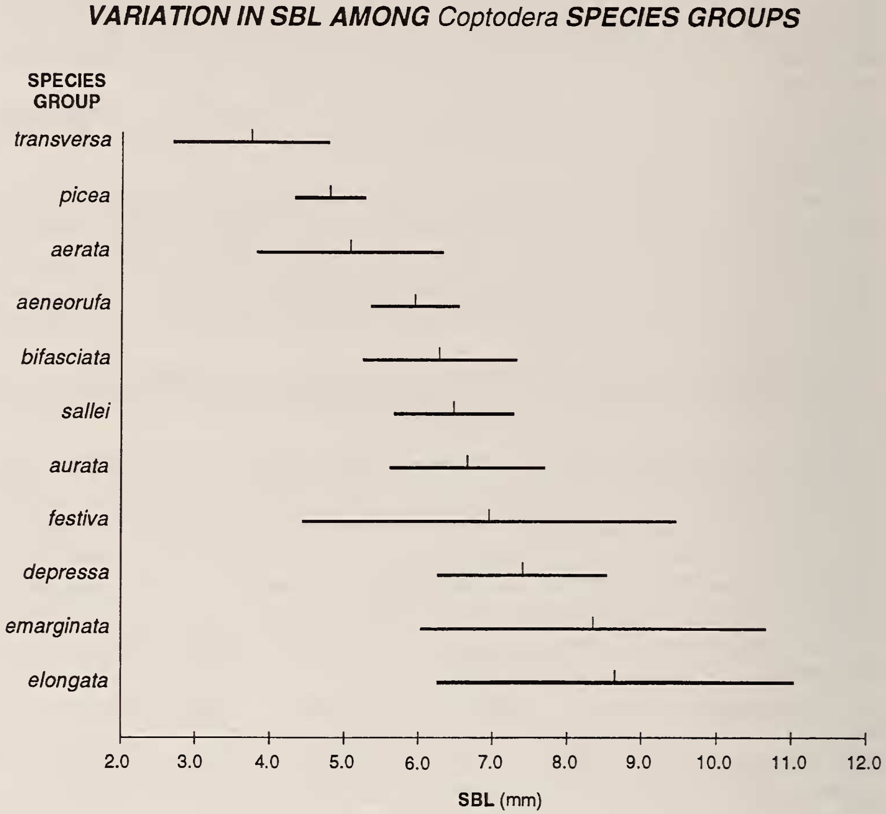


FIGURE 37. Range of variation in Standardized Body Length (in mm) among the New World species groups of the genus *Coptodera* Dejean.

background dark and fasciae pale (Figs. 3A and 3B). Each of these basic types was modified further, as noted below.

Of 26 possible derived patterns (excluding reversals), only seven are known: (1), dark head, pronotum, and elytra (frontispiece, and Fig. 38, 1A; evolved in three groups, independently—*aurata* [lineage M], *emarginata* [lineage M^3], and the *picea-aerata* lineage [R^3]); (2), dark head, dark pronotum, and bicolored elytra (Figs. 20B-F) with pale background and dark fasciae (Fig. 38, 2A; evolved in the *transversa* group once [lineage H^2]); (3), dark head, bicolored pronotum, and bicolored elytra, with dark background (Fig. 38, 3A-3B; evolved twice—once in the *festiva* group [sahlbergi—lineage O^2], and once in the *bifasciata* group [lineage G^3]); (4), bicolored head, bicolored pronotum, and bicolored elytra with background dark (Fig. 38, 3B; evolved five times

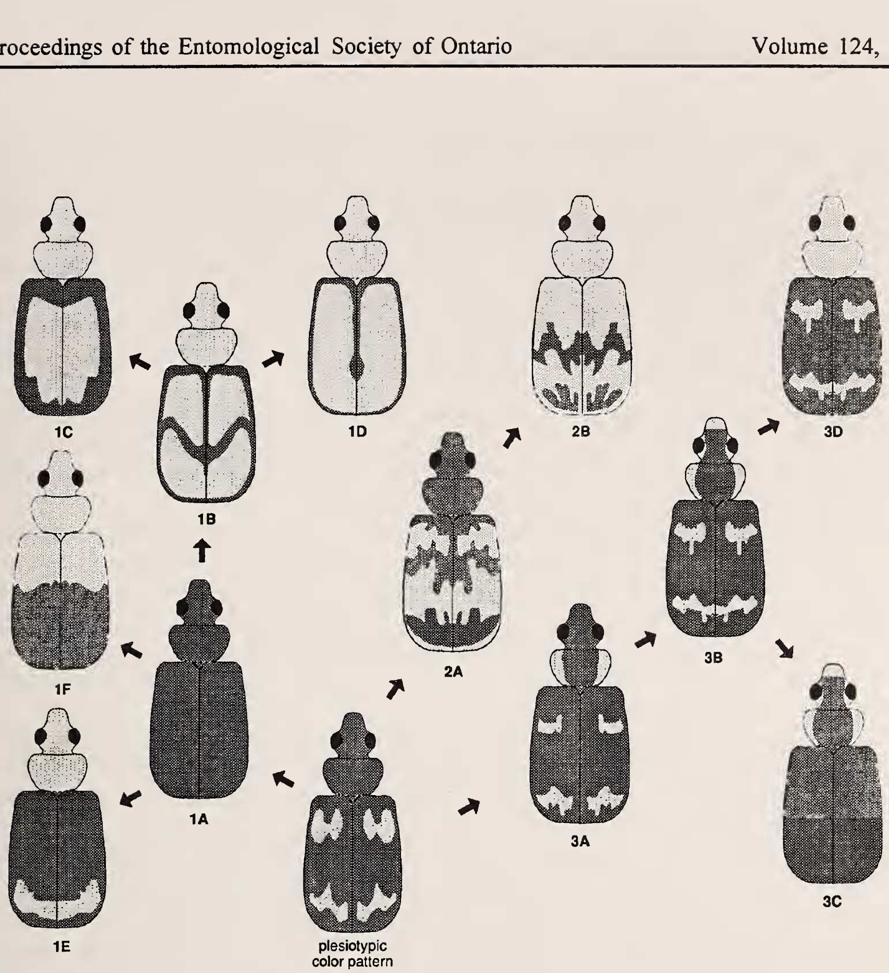


FIGURE 38. Diagram of postulated evolution of color pattern of the dorsal surface among species of the genus *Coptodera* Dejean in the New World.

—three times in the *festiva* group [*relucens*--lineage R^2, *festiva*--lineage U^2, and *teutonica*--lineage B^3], and twice in the *bifasciata* group [*tripartita*--lineage I^3, and *cupreotincta*--lineage K^3]; (5), bicolored head, bicolored pronotum, and dark elytra (Fig. 38, 3C; evolved once, in *aeneorufa* [lineage D^3]); (6), head pale, pronotum pale, and elytra bicolored with dark background (Fig. 3D; evolved four times, twice in the *festiva* group [*C. poecila*--lineage S^2, and *rufescens*--lineage A^3], and twice in the *aerata* group [*nitidula*--lineage V^3, and *waytkowskii*--lineage Z^3]; and (7), head pale, pronotum pale, and elytra bicolored with background pale and fasciae dark (Fig. 2B; evolved once, in the *transversa* group [lineage Z]).

In the *C. aerata* group, partial depigmentation has produced bicolored elytra three times (*C. nitidula* [Fig. 38, 1B-1D; Figs. 33A-C], *waytkowskii* [Fig. 38, 1E; 33D], and *erwini* [Fig. 38, 1F; 33E]). Although the character state "bicolored" is regarded as plesiotypic for the elytra of *Coptodera*, its appearance in the *C. aerata* group is a derived condition, and represents a reversal.

Note, however, that the pattern is not the same as in those taxa with plesiotypically bicolored elytra.

Short, parallel trends in reduction of dark color are represented by the adelphotaxa *C. relucens-poecila* and *C. teutonica-rufescens*: the first member of each species pair has the head and pronotum bicolored, whereas in the second member, these sclerites are completely pale. In general, a trend in reduction of dark pigment is evident in the *C. transversa, festiva, aeneorufa* and *bifasciata* groups. In the *C. transversa* group, pigment reduction of the head and pronotum seems to have been a single step (dark to pale). In the others, a two-step process is evident: from dark to bicolored, and from bicolored to completely pale.

Erwin (1979b: 547) suggests that color and color pattern of arboreal carabids are the result of selection caused by predators. The relatively few combinations that have been realized and the development more than once of some combinations suggest that color pattern is important in the adaptation to their habitats of the species of *Coptodera.*

Sense organs.-- Ventral pits on the flagellar articles that house sensory setae evolved once in lineage T^3 (*C. aerata* group, Figs. 1A-B). Such structures have evolved also in several other groups of lebiines (subtribe Metallicina, and Celaenephina). Other evolution of sense organs involves number, size and position of tactile setae (characters 01, 03, 06, 07, 20, and 23). The long setae on the palpigers (character 01) characteristic of the pericaloid assemblage, must enhance the sensory component of the mouthparts, but the advantages of the other changes affecting sensory organs is not apparent.

Mouthparts.-- Apotypic features of the mouthparts are recorded as 11 characters: 02 (edentate mentum, Figs. 6A-D); 08 (notched anterior margin of labrum, Figs. 1C-H); and 21, 27, 30, 32, 34, 36, 37, and 51 (various aspects of the mandibles, Figs. 2A-H, 3A-L, and 4A-L). Changes in details of mandibular structure include: surface grooving (characters 21, 30, 32, 34 and 36); shortening of the terebra or lengthening of the basal area (character 51); widening of the molar area (character 27); narrowing of the molar groove (character 35); and loss of the ventral groove (character 37). Loss of the ventral grooves was preceded by loss of the ventral microtrichia which probably are involved in transfer to the mouth of liquified bits of prey (Evans and Forsythe 1985: 115). Such loss suggests that the mandibles of *Coptodera* adults are used only for prey capture, or that only particulate matter is transferred to the mouth *i.e.*, that digestion is solely post-oral, and not pre-oral. The system of parallel strigils or grooves on various parts of the occlusal margins might be indicative of improved holding or shredding surfaces. Increase in size of the molar area might have to do with an enhanced crushing ability, crushing being the normal function of this region.

Overall, there is a marked transformation in the mandibles, associated with the reconstructed phylogeny. Among the more primitive lineages (A and its descendants), *C. sallei* exhibits no apotypic features (Figs. 2A-F), and the *aurata* and *elongata* groups exhibit one apotypy each. Of the more basal stocks of the more derived lineages (R and its descendants), the *C. depressa* group (S and its descendants) exhibits two mandibular apotypies, whereas for the remaining taxa (V and its descendants) the number of apotypies ranges from five (*bifasciata* group) to eight (*emarginata*, *picea* [Figs. 4A-F], and *aerata* [Figs. 4G-L] groups). This trend suggests some changes in feeding methods, and possibly in food consumed.

Elytra.-- Surface luster and sculpture of the elytra are discussed above. Here, we note development of spines posteriorly (characters 22 and 26). The postero-lateral angles have become spinose in the *elongata* group (lineage D, Fig. 15A), only. The sutural angles have become spinose three times, once each in the *elongata* (lineage F, Figs. 15B-E), *transversa* (lineage L^2, Fig. 20I) and *emarginata* (lineage O^3,Figs. Figs. 28A-B) groups.

As Erwin (1979b: 552-553) notes, spinose elytra of New World Lebiini are almost confined to tropical arboreal species. He suggests that such spines might have evolved as "antipredation" devices, perhaps functioning to prevent being swallowed by predators.

Legs.-- Excluding setation (see above, under evolution of secondary sexual features), only two features of the legs show variation. The upper spur of the fore tibia (character 44) has been reduced in one lineage (R^3, Figs. 9C-D), and then lost (lineage T^3, Figs. 9F-G). This spine has been lost also from lineage I^2 (*C. transversa*). Pectens of the tarsal claws (character 50) have become markedly reduced in lineage J (*C. championi-apicalis*, Fig. 9B) and in lineage A^3 (*C. rufescens*).

The significance of these changes is not immediately apparent. The upper tibial spur is part of the antenna cleaning organ. Its loss (known to have occurred in other lebiine groups, such as *Lebia* and *Euproctinus*) may indicate a change in function of the cleaning organ. The reduced pectination of the tarsal claws may represent a change in detailed mechanism of gripping the substrate. Perhaps with fewer points of contact of claws with substrate, a beetle is able to move more rapidly, though it might have to avoid smoother surfaces.

Stylomere 2 of the ovipositor.-- Normally, the ensiform setae are located on the dorsal margin of stylomere 2. In the *C. sallei* and *elongata* groups (lineages B and D, respectively), however, probably independently, these setae have shifted to a more lateral position (character 07, Figs. 11A-D). The functional significance of this shift is not apparent.

Secondary sexual characters.-- Six secondary sexual features (characters 17, 29, 33, 38, 39 and 52) are exhibited by males, and one (character 8) is exhibited by females, involving primarily patches of setae, variously distributed. Most of these apotypic states are confined to single groups: 18 (setae on the femora), to the *C. elongata* group (lineage D); 38 and 39 (setal patches on abdominal sterna and metasternum Figs. 9A-B, to the *transversa* group (lineage W); and 52 (adhesive vestiture on tarsomeres of middle legs) to the *bifasciata* group (lineage J^3). Character 17 (setal patches on the ventral surfaces of the fore femora) occurs only in *C. sallei* (Figs. 7A-B) and *C. versicolor* (Figs. 7C-D), each occurrence being an independent development.The apotypic state of character 29 (notched middle tibia of males) and 33 (notched abdominal sternum VII) characterize lineage R and its descendants--the largest assemblage of New World *Coptodera*. Mid-tibial notches are known also in the genus *Lebia* (Madge 1967: 147). Possibly they are used by males as an additional device to hold on to females, gripping the edges of the elytra during mating.

Thus, secondary sexual characters range in distribution from a few to many species. The setal patches could be involved in release of pheromones, while the adhesive devices may provide enhanced ability of males to hold on to females during mating.

Male genitalia.-- The males of each New World species of *Coptodera* exhibit distinctive genitalia, differing variously from their putatively close relatives in form and proportions of the median lobe, position of the ostium, and in size and number of macrospines of the internal sac. Eight characters (numbers 09, 11, 12, 13, 46, 47, 48 and 49) and 54 character states of the genitalia were recognized. Such tendency for interspecific differentiation suggests that, at times in the history of lineages, the genitalia were labile, a suggestion borne out in the remarkable variation exhibited by males of *C. acutipennis*, in which nine morphs are distinguishable.

Position of the ostium (character 09) exhibits distinctive trends, from nearly catopic in the more primitive lineages (descendants of lineage A, Figs. 14B-C, and 16A-J) to anopic (Figs. 34A-H) and pleuropic-right (Figs. 27A-H, and 28C-F) in the most derived lineages (descendants of lineage E^3). Fig. 39 is a diagram, illustrating the hypothesized evolution of this character.

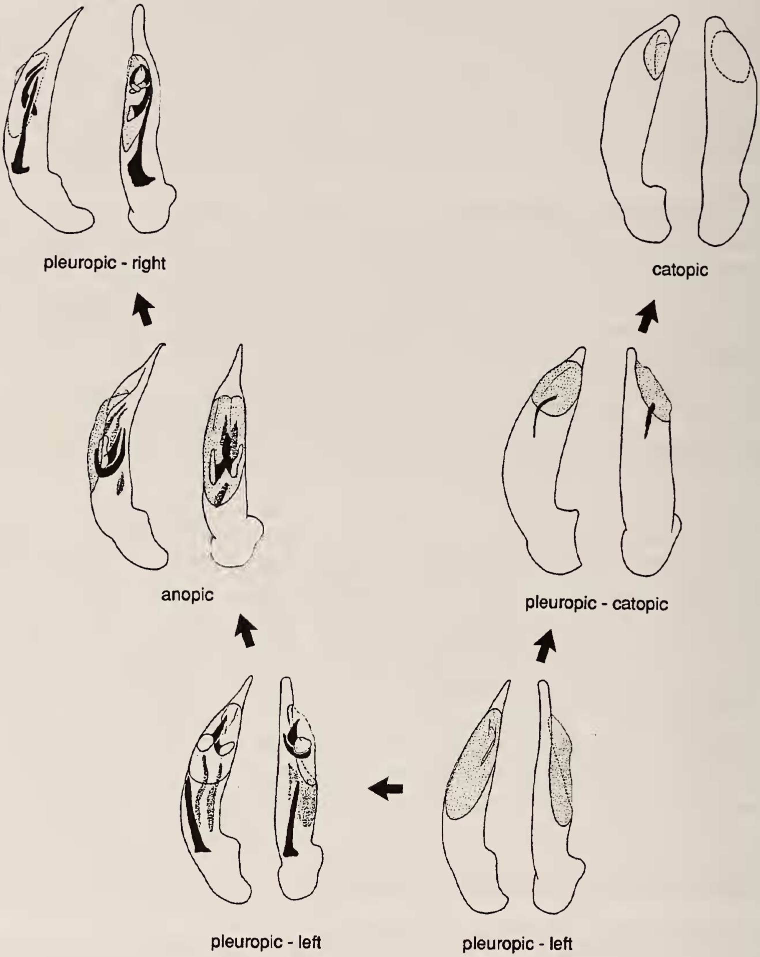


FIGURE 39. Diagram of postulated evolution of the median lobe of the male genitalia among species of the genus *Coptodera* Dejean in the New World.

The more derived lineages (descendants of lineage M ^{2}) are characterized by having macrospines on the internal sac (characters 46-48; cf. Figs. 24A-N). Otherwise, the pattern of genitalic variation seems almost random.

Summary of character evolution.-- The evolutionary pattern overall is simple in that most sequences of change are short, each such involving development of an apotypic state followed by stasis or reversal, and without continued specialization of the apotypy. The evolutionary pattern is complex, however, in terms of convergences and reversals, as indicated in Table XIII and Fig. 36, and as discussed above. Such a pattern may be a reflection of the seemingly slight ecological differentiation of the genus, with lineages being subjected repeatedly to the same kinds of selective forces, but in different combinations in different geographical areas, and under oscillating climatic regimes. The only marked shift in way of life seems to be that of departure from close association with tree trunks and loosened bark to life in the leaf litter and association with fruitfalls. A consistent feature of *C. acutipennis*, and a varying feature of *C. festiva* and *C. cupreotincta*, this ecological change is not accompanied by any striking structural changes.

Why, then, are there so many species of *Coptodera* in the New World? Perhaps this diversity has to do with features related to reproduction rather than those associated with day to day maintenance. Certainly, secondary sexual features characterize the major South American stock of *Coptodera* (lineage R), and the most varied character system is that of the male genitalia; the latter system may be involved with development of reproductive isolation. Thus, geographical isolates may tend to differentiate in such features. That geographical isolation has occurred frequently in the history of *Coptodera* is indicated by distribution patterns of extant taxa, as discussed below.

Geographical history of the New World species of *Coptodera*

Introduction.-- Maps 1-20 illustrate the known geographical ranges of the species of *Coptodera*, and are basic empirical components of this analysis. The theoretical component is the general theory of evolution of distribution patterns of Neotropical taxa that have been developed during the past half century by biogeographers and geologists. For general background information see, in particular, publications by Hershkovitz (1966 and 1972), Whitehead (1976), Schreiber (1978), Noonan (1979), Erwin (1979a), Savage (1982), Stehli and Webb (1985a), and Halffter (1987). For zoogeographical analyses of taxa of Carabidae with ranges comparable to those of *Coptodera*, see references in Noonan (1985), and the discussion below, under "Comparisons".

The distribution pattern of *Coptodera* in the New World is presented in terms of species diversity and postulated interspecific relationships. A general synthesis is based on correlating the chorological patterns and the reconstructed phylogeny of the New World species of *Coptodera*.

TABLE XIV. Diversity of New World species of *Coptodera* Dejean by 10° intervals of latitude.

Latitude	No. Species
40-50 N.	1
30-40 N.	3
20-30 N.	11
10-20 N.	15
0-10 N.	21
0-10 S.	23
10-20 S.	22
20-30 S.	16
30-40 S.	1

The distribution pattern: species diversity.-- Latitudinally, species number is maximal equatorially and decreases north and south, as summarized in Table XIV. Of the 43 known species of *Coptodera*, the ranges of 29 are confined to the tropics. The ranges of 14 species extend beyond the tropics: two (*C. brunnea* and *aerata*), north of the Tropic of Cancer, only; 10, south of the Tropic of Capricorn, only; and two (*C. picea* and *nitidula*), both north of the Tropic of Cancer and south of the Tropic of Capricorn. The range of only one species (*C. aerata*) is completely outside of the tropics (to the north).

The geographical distribution of *Coptodera* was analyzed as well in terms of biogeographical zones or areas (or morphoclimatic domains [Heyer 1988: 265]) that have more or less distinctive assemblages of species of this genus or that have been recognized on the basis of distribution patterns of other taxa (see, for example, Willink 1988: 207, Fig. 1). Each zone, designated by a capital letter, and its approximate geographical limits is indicated in Table XV and on Map 21. Table XVI illustrates species ranges in terms of these zones.

The zones with the largest number of species are: C (Amazon Basin); A (Southern Atlantic Forest and environs); and H (Nuclear Central America). Together, zones A and C have 29 species, or about two-thirds of the New World *Coptodera* fauna.

The species of *Coptodera* occupy from one to 10 zones (Tables XVI and XVII). Nearly half (20) of the species are known from single zones (Table XVII), and of these, 14 are in zones A (Southern Atlantic Forest and environs) and C (Amazon Basin). The remaining single zone precinctives are distributed among five zones. Six zones are without precinctives.

While interpreting these numbers, it is important to consider that seven of these single-zone precinctive species are known from few specimens and each from a single locality (zone A--*C. sigillata*, *squiresi*, and *teutonica*; zone C--*C. pakitza* and *erwini*; zone G--*C. poecila*; and zone J--*C. foveolata*). Almost certainly, the ranges of these species are more extensive, and may extend into other zones. However, it is unlikely that additional information about the ranges of these species will alter the overall patterns appreciably.

At continental and sub-continental levels, Table XVI shows that 23 species are precinctive in South America, and 12 are precinctive in North America, with 10 of the latter in Middle America, only, one in the U.S.A., only, and one shared between Middle America and the southwestern United States. Eight species are shared between North and South America; of these shared species, only three enter United States, and only in the south. In summary, each continent has a distinctive set of species of *Coptodera*, with the precinctives comprising 80 percent (35/43) of the total *Coptodera* fauna.

From an evolutionary perspective, the distribution patterns, interpreted solely in terms of species diversity, indicate three major tropical centers of diversification: two in South America, with one each in the Amazon Basin and Southern Atlantic zone; and one center in tropical North America (*i.e.*, Middle America).

The distribution pattern is consistent with a major barrier between North and South America. With the West Indies having been invaded by only two species, and with *trans*-Andean South America (zone F) having only four species in contrast to the extensive *cis*-Andean assemblage, the distribution pattern is consistent with a group whose members do not cross readily open sea or extensive mountain ranges.

The distribution pattern: phylogenetic aspects.-- If differentiation of lineages has a geographical component, the latter is identified by examination of chorological affinities of related taxa. Adelphotaxa that occupy different areas point to previous connections between those areas.

TABLE XV. Zoogeographic zones for description of geographical ranges of the New World species of *Coptodera* Dejean.

Zone	
A	Southern Atlantic South America, south and east of the Amazon Basin. This corresponds approximately to the area containing the Serro do Mar and Paranese biotas (see Nores [1992: 347, Fig. 1]), or the Atlantic Forest (Vanzolini 1988: 327), and includes principally semideciduous or seasonal forest, and "rich dense forest on rolling terrain" (Brown 1982: 293, Fig. 16.33).
B	*cis*-Andean South America (Vanzolini 1988: 317), south of the Amazon Basin (*Ca.* 20°S.), between the eastern slopes of the Andes and the Southern Atlantic Zone (A). This corresponds to the dry areas between Zones A and C, and includes the Chaco, Cerrado, and Caatinga (Nores 1992: 347, Fig. 1).
C	The Amazon Basin. The general term for the forests of this great area is hylaea. In fact, the hylaea extends unbroken from the Amazon Basin to the Guianas (Vansolini 1988: 326).
D	*cis*-Andean South America, north of the Amazon Basin and west of the Northern Atlantic Zone (E).
E	*cis*-Andean South America, north of the Amazon Basin and including northern Brazil and the Guianas (the North Atlantic Zone).
F	Chocó refugium in *trans*-Andean Columbia and Ecuador (see Gentry (1982) for a discussion of the flora of this region).
G	Lower Central America, including Panamá, north to southern Nicaragua.
H	Nuclear Central America, from Northern Nicaragua to the Isthmus of Tehuantepec, in southern México.
I	México north of the Isthmus of Tehuantepec, Pacific Versant.
J	México, north of the Isthmus, Gulf (or Atlantic) Versant.
K	West Indies
L	Southwestern United States (Arizona and New Mexico)
M	Eastern United States, from Florida west to the 100th Meridian, and north to about 43°N.

DISTRIBUTION OF THE NEW WORLD SPECIES OF *Coptodera* IN RELATION TO GEOGRAPHICAL ZONES

		GEOGRAPHICAL ZONES																
MAP No.	SPECIES	SOUTH AMERICA						MIDDLE AMERICA				WEST INDIES	U. S. A.		TOTAL ZONES OCCUPIED	PRECINCTIVE IN :		SHARED BETWEEN S.A.& N.A.
		A	B	C	D	E	F	G	H	I	J	K	L	M		SOUTH AMER.	NORTH AMER.	
8	*fulminans*	▨													1	▨		
10	*sigillata*	▨													1	▨		
10	*squiresi*	▨													1	▨		
12	*teutonica*	▨													1	▨		
14	*bifasciata*	▨													1	▨		
14	*braziliensis*	▨													1	▨		
12	*rufescens*	▨				▨									2	▨		
14	*tripartita*	▨		▨											2	▨		
6	*depressa*	▨	▨		▨										3	▨		
11	*sahlbergi*	▨	▨	▨											3	▨		
7	*dromioides*	▨	▨	▨		▨									4	▨		
15	*emarginata*	▨	▨	▨		▨									4	▨		
6	*versicolor*			▨											1	▨		
8	*nigrosignata*			▨											1	▨		
11	*relucens*			▨											1	▨		
11	*pakitza*			▨											1	▨		
15	*chalcites*			▨											1	▨		
20	*waytkowskii*			▨											1	▨		
20	*erwini*			▨											1	▨		
3	*megalops*			▨											1	▨		
9	*nigrostriata*			▨		▨									2	▨		
13	*aeneorufa*			▨		▨									2	▨		
4	*apicalis*						▨								1	▨		
10	*stockwelli*							▨							1		▨	
11	*poecila*							▨							1		▨	
2	*elongata*							▨	▨		▨				3		▨	
9	*lineata*							▨	▨	▨	▨				4		▨	
12	*festiva*			▨				▨	▨	▨	▨	▨		▨	7		▨	
1	*sallei*								▨		▨				2		▨	
5	*xanthopleura*								▨	▨					2		▨	
5	*aurata*								▨		▨				2		▨	
12	*nigroviridis*								▨		▨				2		▨	
18	*brunnea*								▨		▨		▨		3		▨	
5	*viridis*									▨					1		▨	
12	*foveolata*										▨				1		▨	
19	*aerata*													▨	1		▨	
14	*cupreotincta*	▨		▨				▨	▨		▨				5			▨
10	*transversa*	▨	▨	▨	▨			▨	▨	▨	▨				8			▨
15	*acutipennis*	▨		▨	▨	▨	▨	▨	▨		▨				8			▨
16	*picea*	▨	▨	▨	▨	▨		▨	▨		▨	▨		▨	10			▨
17	*nitidula*	▨	▨	▨		▨	▨	▨	▨	▨	▨		▨		10			▨
3	*schaumi*			▨	▨			▨	▨						4			▨
4	*championi*						▨	▨							2			▨
	TOTAL SPECIES	17	7	21	5	8	4	12	14	6	13	2	2	3		23	13	7
	TOTAL PRECINCTIVES	6	0	8	0	0	1	2	0	1	1	0	0	1		23	13	0

TABLE XVI. Distribution of the New World species of *Coptodera* in relation to geographical zones.

TABLE XVII. Frequency distribution of number of New World species of *Coptodera* Dejean and number of zoogeographic zones occupied (see Table XVI for details).

No. Zones Occupied		No. Species
1		20
2		9
3		4
4		4
5		1
6		0
7		1
8		2
9		0
10		2
	Total No. Species	43

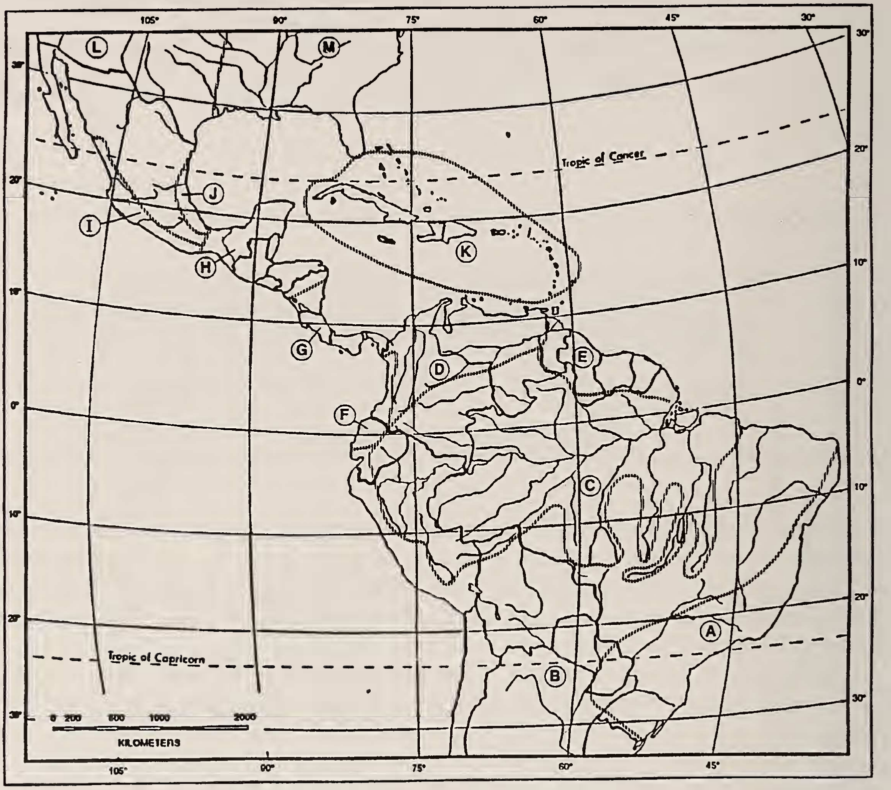
Figure 35 shows generally a broad overlap among species groups of New World *Coptodera*, indicating for most of them extensive sympatry. However, the concentration of the descendants of Lineage A in the Middle American part of North America, and conversely the concentration of descendants of lineage R in South America, is indicative of a barrier in the past between the North and South American continents.

At the level of species, in contrast, Table XVIII shows allopatric associations among eight of the 11 pairs. Putative barriers within zone A would explain the distribution of two pairs. The ranges of two pairs, though overlapping broadly or narrowly, differ sufficiently to suggest a barrier between zones A and C. A barrier between South America and Middle America would explain the chorological affinities of four pairs of allopatric species, and two pairs of species with ranges that overlap broadly or narrowly. A barrier between zones I and J would explain the chorological affinities of one species pair.

Table XIX shows the distribution pattern for second and third level groupings of taxa. For each set of adelphotaxa, each component is numbered for ease of reference. Of 14 comparisons, seven, or half, are allopatric associations, and three are narrowly sympatric. The incidence of allopatry is lower than among species pairs, but allopatry is an important component of the pattern.

Location of putative barriers among adelphotaxa is instructive: four are between zones A and C; four are between South America and Middle America; one is within zone C; one is between Lower and Nuclear Central America; and one is within zone J, on the Gulf Versant of México. As for species pairs, the putative barrier between South and Middle America is prominent for these more inclusive groups of taxa.

Summary of the evidence.-- The New World species of *Coptodera* are basically tropical, being confined to lowland and lower montane forests. Most of the species are South American, and many of the species are precinctive there. There is also a substantial Middle American fauna of *Coptodera*, with a precinctive component. The West Indies archipelago harbors only two wide-ranging species. North America north of México is marginal for the genus, with a single precinctive species in zone M.



MAP 21. Biogeographic zones for the New World species of *Coptodera* Dejean.

Although geographical ranges overlap broadly at the level of species groups, the descendants of the basal lineages (A and R) are concentrated in Middle America and South America, respectively. Within the groups allopatry and narrow sympatry are prominent features of the distribution pattern.

Based on this pattern, the following scenario is offered group by group as a reconstruction of the geographical history of *Coptodera* in the New World. The discussion is followed best by referring to the maps and to the reconstructed phylogeny (Fig. 36).

The process of development of the distribution pattern of *Coptodera* in the New World.--Because the genus is basically Gondwanian in distribution, we postulate that the ancestral stock was part of the original South American biota, when the South American continent separated from Africa during Mesozoic time. Late in the Cretaceous period, or early in the Tertiary, an early stock of *Coptodera* reached the Middle American part of North America. South America and southern North America were either joined temporarily then, or inter-continental access was easier than it was subsequently (Fig. 40), until the development of a permanent land connection during

TABLE XVIII. Species-level adelphotaxa of the New World species of *Coptodera* Dejean and their chorological affinities.

SPECIES - LEVEL ADELPHOTAXA AND THEIR CHOROLOGICAL AFFINITIES

MAP No.	SPECIES PAIRS	GEOGRAPHICAL ASSOCIATION Broadly Sympatric	Narrowly Sympatric	Allopatric	PUTATIVE BARRIERS OR AREAS OF CONTACT
10	*sigillata - squiresi*			▨	within zone A
12	*rufescens - teutonica*			▨	within zone A
6	*depressa - versicolor*	▨			between zones A & C
15	*emarginata - acutipennis*		▨		between zones A & C
11	*relucens - poecila*			▨	S. America / M. America
3	*schaumi - megalops*			▨	S. America / M. America
4	*championi - apicalis*			▨	S. America / M. America
9	*lineata - stockwelli*			▨	S. America / M. America
17-18	*nitidula - brunnea*	▨			S. America / M. America
19-20	*waytkowskii - aerata*			▨	S. America / M. America
5	*aurata -viridis*			▨	between zones I & J
	Total	2	1	8	

TABLE XIX. Two- and three-level adelphotaxa or trichotomous relationships, and their chorological affinities.

TWO - AND THREE - LEVEL ADELPHOTAXA OR TRICHOTOMOUS RELATIONSHIPS, AND THEIR CHOROLOGICAL AFFINITIES

MAP No.	COMPONENTS OF SPECIES COMPLEXES 1	2	3	GEOGRAPHICAL ASSOCIATION Broadly Sympatric	Narrowly Sympatric	Allopatric	PUTATIVE BARRIERS OR AREAS OF CONTACT
14	*bifasciata*	(*tripartita*	(*cupreo. + braz.*))	1 & 3	1 & 2 ; 2 & 3		1 / 3 - A / C ; 1 / 2 - A / C
10	*transversa*	(*sig. + squiresi*)			1 & 2		A / C
15	*chalcites*	(*emarg. + acut.*)		1 & 2			A / C
12	*nigroviridis*	(*ruf. + teutonica*)				1 & 2	M. Amer. / S. Amer.
9	*nigrostriata*	(*lin. + stockwelli*)				1 & 2	M. Amer. / S. Amer.
8-9	*nigrosignata*	(*fulminans*	(*nigst. - (lin. + stock.*))	2 & 3		1 & 2 ; 1 & 3	2 / 3 - C ; 1 / 2 - A / C ; 1 / 3 - S. Amer. / M. Amer.
12	*foveolata*	(*nigroviridis*	(*ruf. + teutonica*))			1 & 2 + 3 ; 2 & 3	1 / 2 + 3 - H / J ; 2 / 3 - M. Amer. / S. Amer.
2-4	*elongata*	((*sch. + meg.*)	(*champ. + apicalis*))	2 & 3		1 & 2 + 3	1 / 2 + 3 - S. Amer. / M. Amer.; 2 / 3 - C-D / F
			Total	4	3	7	

the Pliocene epoch (Savage 1982). Following entry into Middle America, the New World stock of *Coptodera* differentiated into a Middle American component (lineage A) and a South American component (lineage R, Fig. 35).

Coptodera sallei (lineage B, Map 1) is interpreted as a phylogenetic relict, occupying montane tropical forests on the Pacific Versant of Guatemala and on the Gulf Versant of México. The fact that this species occurs at higher altitudes only (between 1200 and 1900 m.) suggests that it has been displaced from the lowland forests that are occupied by the other species groups of *Coptodera*.

The *elongata* group (lineage D) probably differentiated first into a Nuclear American component (lineage E, Map 2), represented by *C. elongata*, and a Lower Central American-South American component, lineage F. The ranges of the descendants (lineages G and J) of the latter (Maps 3 and 4) extend into the Amazon Basin (zone C) in *cis*-Andean South America, and into the Chocó (zone F) in *trans*-Andean South America.

We postulate an initial South American differentiation for lineage F: first, a barrier oriented north-south (the Andes?) to separate descendant lineages G and J, with G to the east and J to the west. Then, we postulate a barrier oriented east-west, and that this barrier was the seaway between South America and the early Tertiary volcanic islands that comprised Lower Central America. This postulate requires a crossing of the sea barrier by both lineages G and J, with consequent differentiation of each lineage into two species. Finally, the more northern descendants, *C. schaumi* and *C. championi* that were the islandic isolates, invaded South America comparatively recently (Fig. 40). Other scenarios are possible, particularly differentiation of lineages G and J in South America, with the more northerly pair of descendants (*C. schaumi* and *C. championi*) invading Middle America comparatively recently, using the Panamanian land bridge to do so. We chose the former hypothesis because it uses a ready-made barrier—a barrier that is not so apparent on the South American continent.

Differentiation of lineage M (*aurata* group, Map 5) occurred in Middle America. The location of the barrier that produced descendant lineages N (*C. xanthopleura*) and O is not evident. Disjunction of lineage O, however, probably was associated with the orogenic events that produced the Mexican highlands in Miocene time (Kohlmann and Halffter 1990: 12), isolating ancestral *C. aurata* in the east (zone J) and ancestral *C. viridis* in the west (zone I).

Differentiation of lineage S (*depressa* group, Map 6) evidently had to do with development of a disjunction between the forests of the Amazon Basin (zone C) and those of the Southern Atlantic zone (zone A), producing in zone C ancestral *C. versicolor*, and in zone A ancestral *C. depressa*. Subsequently, *C. depressa* became more widespread, if the widely disjunct records in Colombia and Trinidad can be accepted at face value.

Differentiation of lineage X (*transversa* group, Maps 7-10) is highly complex, suggesting a sequence of disjunctions followed by differentiation and subsequent range interpenetration. Because of extensive range overlap of the various lineages and the consequent difficulty of attempting to postulate locations of range disjunctions and barriers, we confine a detailed consideration to lineages C^2 (Map 9) and H^2 (Map 10). Each of these lineages is represented in both South America and Middle America.

The species of lineage C^2 are allopatric in relation to one another, and their ranges form a line suggesting disjunctions that paralleled the reconstructed phylogeny. A disjunction between South America and Lower Central America separated lineage D^2 (ancestral *C. nigrostriata*) from lineage E^2. Subsequently, the range of the latter was divided by a barrier (probably in Lower Central America) that led to development of the extant *C. lineata*, which ranges from zone G to I and J, and *C. stockwelli*, known only from zone G, to the east of the range of *C. lineata*.

The species of lineage H^2 range over much of the same territory occupied by the species of C^2. However, all three species of H^2 are represented in the South Atlantic zone A, and it seems likely that their ranges overlap there, at least partly. A possible scenario for the differentiation of these species is the following: isolation of segments of lineage H^2 in the Amazon Basin (zone C) and the South Atlantic zone (A), the Amazonian isolate giving rise to *C. transversa*, and the South Atlantic isolate to ancestral lineage J^2. Subsequently, the range in zone A of the latter lineage was divided, the resulting isolates giving rise to the extant species *C. squiresi* and *C. sigillata*. Later, the Amazonian *C. transversa* dispersed: northward and westward, to enter and become widespread in Middle America; and southward and eastward, to enter zone A. Its apparent confinement in México to the Gulf Versant (zone J) suggests arrival there in post-Pliocene time (Halffter 1974: 227).

Lineage N^2 (*festiva* group, Maps 11 and 12) groups nine species, the combined ranges of which include all of the zoogeographic zones except L to the north, and *trans*-Andean zone F. Although *C. festiva* is on both American continents, we postulate that it is adventive in South America, being an immigrant there, or more probably, an introduction—it is known only from a locality near the mouth of the Amazon River (Map 12), and easily could have been carried there in a ship from a Caribbean port.

Lineage N^2 differentiated into O^2 (*C. sahlbergi*) and P^2, with *C. sahlbergi* centered in the South Atlantic zone (A), and probably isolated there as an early disjunct. Lineage P^2 probably occupied the Amazon Basin (zone C) and adjacent areas. The disjunctive event that led to differentiation of the latter lineage into Q^2 and T^2 probably was entrance by dispersal of the lineage into Middle America (specifically zone G, Lower Central America). The South American descendant lineage also, but subsequently, entered Lower Central America (zone G), giving rise there to lineage S^2 (ancestral *C. poecila*) and the South American vicar R^2 (in zone C), giving rise to ancestral *C. relucens*.

The Middle American lineage, T^2, differentiated sequentially to produce five extant species, two of which (*C. rufescens* and *teutonica*) are South American precinctives, in zones E and A. The localities of two of the Middle American species (*C. foveolata* and *nigroviridis*) are in zones H and J, in México, and are overlapped by the range of widespread *C. festiva* (Map 12). Probably differentiation was through disjunction, with *C. festiva* invading subsequently the ranges of its relatives.

The adelphotaxon of *C. nigroviridis* (lineage Y^2) is lineage Z^2, the ancestral stock of *C. rufescens* + *teutonica*. Evidently the common ancestor of these lineages (X^2) became widespread, dispersing southward into South America, and then eastward. With *C. rufescens* and *C. teutonica* being represented in very few localities, further comment about their differentiation is not justified.

Lineage C^3 includes the extant members of five species groups of *Coptodera* (*aeneorufa*, *bifasciata*, *emarginata*, *picea* and *aerata* groups), whose ranges are indicated on Maps 13 to 20. Most of the species are South American, and so we postulate that most of the species level evolution has taken place in South America.

The monobasic *aeneorufa* group (lineage D^3, Map 13) is widespread in the Amazon Basin, and as well enters the Guianas (zone E). Its adelphotaxon, lineage E^3, contains most of the species. The immediate descendants of lineage E^3 (F^3 and R^3) include two groups, each of which has representatives in Middle America.

The four species of lineage G^3 (*bifasciata* group, Map 14) are represented in zone A. However, *C. braziliensis* and *C. bifasciata* are known only from this zone, and their contact with the other two species, *C. tripartita* and *C. cupreotincta*, is marginal. Thus, it seems reasonable to postulate range disjunction as a means of speciation: isolation of lineage I^3 (*C. tripartita*) in the

Amazon Basin, and isolation of lineage J^3 (possibly in zone A, to the southeast), followed by dispersal and differentiation to produce ancestral *C. braziliensis* in zone A, and *C. cupreotincta* elsewhere, with the latter becoming widespread, and dispersing as far north as Nuclear Central America (zone H).

Lineage M^3 includes the three species of the *emarginata* group (Map 15). The ranges of the species pair *C. emarginata-acutipennis* (lineage O^3) are in contact marginally in zone E and probably A, with *C. acutipennis* distributed widely to the north and west, including Nuclear Middle America (zone J). The range of *C. chalcites* (lineage N^3) is in principally the Amazon Basin. We postulate a range disjunction separating N^3 and O^3, with N^3 giving rise to *C. chalcites* in the Amazon Basin, and lineage O^3 developing elsewhere, possibly in zone A. Following this differentiation, lineage O^3 became widespread, then disjunct, with the resulting isolates differentiating into the extant species *C. emarginata* and *C. acutipennis*. This latter disjunction could have occurred again between zones A and C, just as the previous disjunction that gave rise to lineages N^3 and O^3. The Amazonian range of *C. chalcites* was overlapped eventually by that of *C. acutipennis*, of lineage O^3.

Lineage R^3 includes two species groups (*picea* and *aerata*) and the most widespread species in the genus (Maps 16-20). The continent of origin of the lineage cannot be postulated directly on the basis of numbers clues: two of the descendants are precinctive species in North America; two are precinctive in South America; and two are widespread. Phylogenetically, two lineages (U^3 and W^3) have vicars on both continents. However, the distribution pattern of lineage R^3 is sufficiently similar to those of the other groups of *Coptodera* that some inferences are possible.

The monobasic *picea* group (lineage $S^{3,}$ Map 16) probably originated in South America, became widespread recently, probably in post-Pliocene time, reaching the West Indies and even southern Florida, probably overwater, from Cuba (Fig. 40).

Lineage U^3 (Maps 17-20) became widespread initially, and produced two isolates: one in Nuclear Middle America (*C. brunnea*, Map 18) and one probably in South America (*C. nitidula*, Map 17). Subsequently, both taxa became more widespread, with *C. brunnea* reaching southwestern United States (zone L), and *C. nitidula* overlapping the range of *C. brunnea*, to the north. Again, the wide range of *C. nitidula* is consistent with rapid spreading northward in post-Pleistocene time (Fig. 40).

Lineage X^3 (Maps 19 and 20) followed a sequence similar initially to that of U^3, except that the two vicars (*C. aerata* precinctive in zone M, eastern United States; and *C. waytkowskii*, possibly precinctive in zone C, the Amazon Basin in tropical South America) remain separated widely. The relationships of *C. erwini* have not been determined, but probably this species is close to *C. waytkowskii.*

Summary.-- The process of diversification of *Coptodera* in the New World has been one of differentiation of geographically isolated vicars, followed by dispersal and range interpenetration of the resulting adelphotaxa. The isolation leading to differentiation has been the result of two processes: interruption of range continuity of beetle species through interruption of habitat continuity principally within South America and Middle America; and crossing of sea barriers, principally between South America and Lower Central America, by dispersing stocks. The intercontinental sea barriers probably varied in extent through time. Disruption of habitat seems to have been a recurring event, with disjunctions being repeated between adjacent zones—in particular, between zones A and C. Present intercontinental range continuity of several extant species is the result of development of a land connection between continental South America and North America (Fig. 40).

Fig. 40, which is based on the presentation above, shows 14 dispersals from South America to Middle America, and four dispersals in the opposite direction. Most of the dispersals are postulated to be relatively recent, occurring during the last few million years or so. The predominance of the south-north direction is consonant with Darlington's (1959) general theory of the direction of movement of species being from larger to smaller land areas.

Comparisons.-- In this section, to illustrate similarity in distribution, we compare the biogeographic patterns of *Coptodera* with the patterns exhibited by the following carabid taxa.

The precinctive New World pericaline eucheiloid complex (Tribe Lebiini), analyzed by Ball and Shpeley (1983: 801-803), like *Coptodera*, was postulated to have had as its principal place of evolution the South American continent. Incursions into Middle America were postulated to have occurred at various times during the Tertiary and Quaternary periods, the earlier lineages to have arrived being represented now by precinctive taxa, in Lower and Nuclear Central America, and in México north of the Isthmus of Tehuantepec. Because the species were represented by very few specimens, especially in South America, a more detailed analysis there of chorological associations and identification of possible areas of precinctivism was not possible.

With the Neotropical indigenous metallicine genus *Euproctinus* Leng and Mutchler (Tribe Lebiini), *Coptodera* shares: a Gondwanian origin (the adelphotaxon of *Euproctinus* is in the Old World Tropics [Ball and Shpeley 1986: 334]); an early differentiation, based on early entry into Middle America, and subsequent evolution there (Ball and Shpeley 1986: 339); recognition of biogeographic zones A, D, F, G, H, I, L and M, based on precinctive or indigenous taxa; postulated recent arrivals in Middle America of representatives of South American taxa; and representation in the West Indies by recent arrivals.

With the pan-tropical genus *Galerita* Fabricius (*sensu latiore*), *Coptodera* shares a vicariant splitting, isolated descendants in Old and New Worlds, and a subsequent early arrival and isolation in Middle America of a primitive stock that gave rise to subgenus *Progaleritina* Jeannel, the South American vicar becoming the subgenus *Galerita* (Ball 1985: 315). The distribution pattern of the predominantly South American and moderately diverse *americana* group has not been analyzed in sufficient detail, either phylogenetically or geographically, to make useful comparisons with other taxa, except to note Middle American taxa that suggest descendence from early arrivals, and species shared between South and Middle America suggesting recent arrival in the latter area. The Middle American subgenus *Progaleritina*, however, has been analyzed. Like *Coptodera*, *Progaleritina* has precinctive species in zones I, J, and M (Ball and Nimmo 1983: 307, Fig. 7).

With the pattern of the New World precinctive harpaline *Stenomorphus* complex of genera, *Coptodera* shares: a splitting of an early stock that gave rise in Middle America to a distinctive group (*Stenomorphus* Dejean) and in South America to its adelphotaxon (*Trichopselaphus* Chaudoir) (Ball, Shpeley and Currie 1991); indigenous components in zones G, I, and J; and later inter-continental dispersals of lineages of both genera (Ball 1978 and 1987).

The New World precinctive harpaline genus *Amblygnathus* Dejean shares with *Coptodera* evidence of an early South American/ Middle American differentiation, with the *A. iripennis* group being indigenous on the North American continent (Ball and Maddison 1987: 274). Like lineage A of *Coptodera*, the *A. iripennis* group became moderately speciose, and like the *C. aurata* species group, it produced a precinctive lineage (the *A. interior-evansi* stock) in zone I (the Pacific Versant of México). As well, there are indigenous species of *Amblygnathus* ranging within zones G and H.

The Australian-New World pterostichine genus *Loxandrus* LeConte shares with *Coptodera* a major species radiation in tropical South America, with lineages of various ages entering the North American continent, and differentiating therein. Zone I has a precinctive species, *L.*

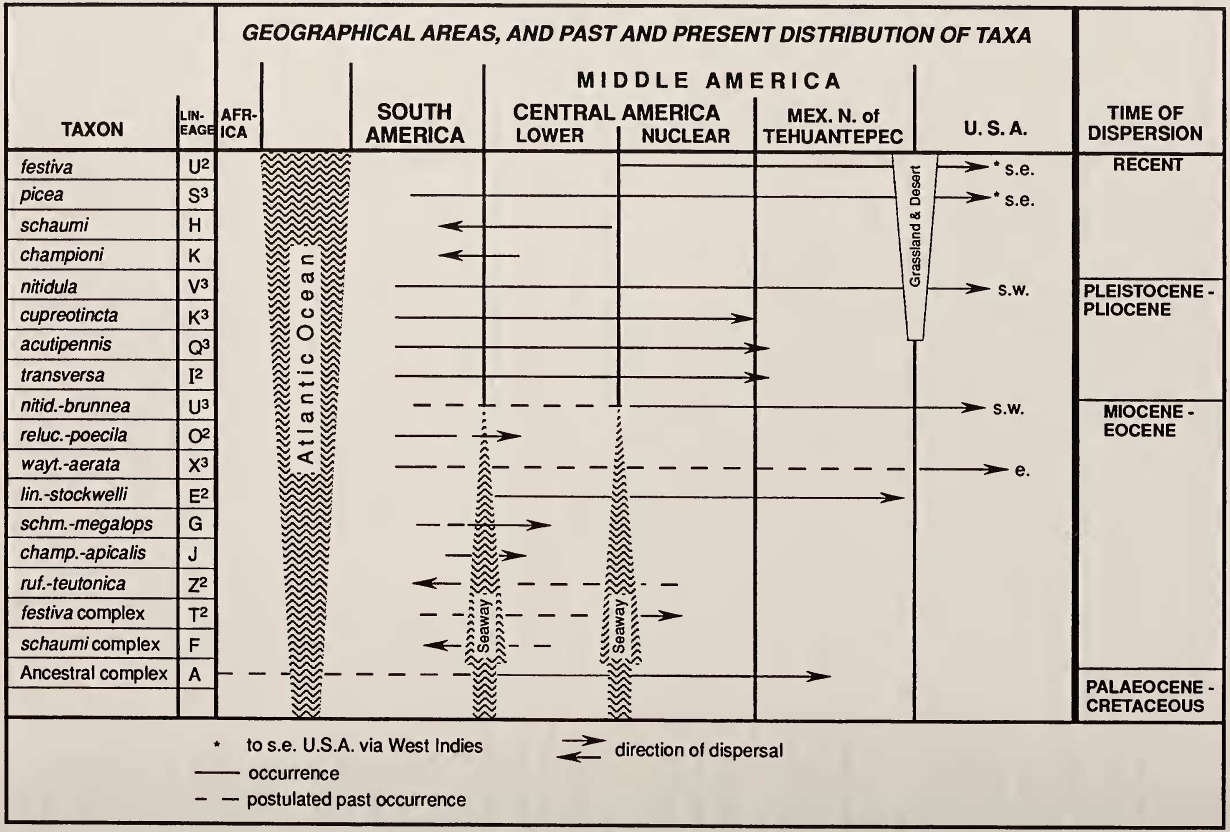


FIGURE 40. Diagram indicating postulated time and direction of intercontinental dispersals of New World species and species complexes of the genus *Coptodera* Dejean.

pactinullus Allen, and zones G, H, and J have indigenous species some of which may be single zone precinctives (Allen and Ball 1980).

In contrast to *Coptodera*, there was a major earlier Tertiary species radiation in zone M (eastern United States), whereas *Coptodera* is represented there by a single precinctive species, *C. aerata*.

Like *Coptodera*, the New World precinctive lebiine genus *Agra* Fabricius consists of arboreal species. It is markedly speciose, with an enormous South American component, but with substantial representation in Middle America, as well. Thus, *Agra* is similar to *Coptodera* in the general pattern of diversity. The genus is being studied in detail by T.L. Erwin, who has produced a series of revisions of various species groups. Only the *A. feisthameli* and *formicaria* lineages have been analyzed zoogeographically (Erwin and Pogue 1988). Both of these complexes exhibit patterns similar to those of *Coptodera*, with precinctive species in zones A, C, G + H + J, and I, referred to by Erwin and Pogue as centers of endemism. The reconstructed phylogeny indicates that descendants of the less derived lineages in Middle America have reinvaded South America, and differentiated there. This is similar to but more extensive than the biogeographical pattern of lineage T^2 of *Coptodera.*

These comparisons point to a general theme underlying evolution of taxa in the Neotropical Region. However, it is important to appreciate that each of the above-noted groups exhibits features of distribution that do not coincide with the distributional features of the other taxa. Probably each taxon responds in a distinctive manner to the forces and circumstances that determine the underlying theme—that response being determined by vagility and a unique combination of other adaptations (Noonan 1988: 366).

General paradigm of Neotropical biogeography.-- For the evolution of the tropical component of the Neotropical biota, a general explanation is emerging, based on refuge theory (Prance 1982 and references therein; Vanzolini and Heyer 1988 and references therein), and on a theory of physical and biotic connections between the North American and South American continents, including when such events took place (Stehli and Webb 1985a and references therein). These theories primarily apply to events that took place during the Cenozoic Era.

Another part of the general explanation of the evolution of the tropical component of the Neotropical biota concerns its origin. The Mesozoic-age supercontinent Gondwana is postulated to be the source area for most of the indigenous South American biota (Jeannel 1942; Noonan 1985: 336-337; Reichardt 1979).

The distribution pattern of *Coptodera* fits rather well the patterns recognized for other taxa, including temporal aspects, and strengthens thereby the general paradigm that has been developing. At the species level, many pairs of inferred adelphotaxa are distributed vicariously in lowland forest in the American tropics, suggesting surviving isolates of once more widespread lineages. Lineages inferred to be older have members that are sympatric with one another, leading to the inference that following differentiation in isolation, dispersal and range interpenetration took place. This suggests that the conditions changed (or ameliorated) that led initially to range disruption, and that the species of *Coptodera* were parts of biotic assemblages (if not integrated communities) and moved as elements of these assemblages. Such alternating sequences of dispersal and range disjunction are tenets of refuge theory, as explained and developed during the past two decades or so (Haffer 1982: 9). There are problems with the refuge theory (see Heyer 1988: 268 and Cadle and Patton 1988: 242), but it seems sound generally.

Middle America houses the principal tropical component of the North American biota. A substantial part of the Middle American biota is postulated to be South American in origin, and this postulate implies dispersal from one area to the other. Changes in intercontinental connections have determined to some extent the timing of arrivals. In fact, the South American component of the Middle American biota consists of older and younger assemblages (Savage 1982: 473 and 477), with older elements (Savage's "Middle American Element") having arrived in Middle America in Late Cretaceous-Palaeocene time, across some form of connection that allowed easier access than was available during most of the subsequent Tertiary Period. That older component differentiated to a more or less marked extent. The present connection of the American continents was established in the late Tertiary (Stehli and Webb 1985b: 11), with the formation of a land bridge, permitting easier access than was possible with the two continents separated by a seaway. This Panamanian land bridge was used by the younger assemblage of taxa (Savage's "South American element") to enter Middle America. (According to Stehli and Webb, the Panamanian connection led to a major biotic intercontinental exchange. For a different point of view about "the Great American Interchange", and one that is more consonant with the facts of distribution of poikilothermous vertebrates and arthropods, see Hershkovitz 1966 and 1972).

As indicated above, and in conclusion, the distribution pattern of *Coptodera* fits generally this theory of a concentration in two time periods of South American lineages entering Middle America, but with the important exception that intercontinental exchange of lineages was not restricted to the periods of easier access. A number of the lineages must have entered both Middle America and South America in periods when the physical connection was interrupted by the Bolivar trench, and Lower Central America was at most a string of isolated islandic volcanos (Duellman 1979; Smith 1985: 41-43).

Concluding Remarks

When we began study of the New World species of *Coptodera*, we planned only a taxonomic treatment at the species level, intending to provide a synopsis that would be useful for identification. In the course of our work, which followed on from the analyses of two great 19th Century carabid specialists, H.W. Bates and M. de Chaudoir, both of whom published their major works on the genus in 1869, we discovered a certain amount of new synonymy, and 12 species previously unrecognized and unnamed—about 27 per cent of the total number of species recognized by us.

As information accumulated about the species, their structural features and geographical distribution, patterns began to emerge, and we were able to develop a system of hypotheses about evolutionary relationships and geographical history of *Coptodera* in the New World. We hope that these hypotheses will be useful to future workers, who will extend knowledge of this genus in holomorphological depth and in geographical breadth.

Although it is possible now to identify to species the adults of *Coptodera* from the New World and from the Afrotropical Region, the same cannot be stated about the species of the Oriental Region. Jedlička's publication (1963) is defective, but at least it provides a starting point. Habu (1967), with his fine work on the Japanese component of the *Coptodera* fauna of the eastern Palaearctic Region that is a northern extension of the Oriental fauna, has provided an excellent basis for work on the latter, and an excellent example of a taxonomic study of high quality. Darlington (1968), working on the New Guinea fauna, has clarified knowledge about the eastern end of the Oriental *Coptodera* fauna.

Once the Oriental species are known to a level of detail comparable to knowledge of the group from elsewhere, it will be possible to provide a general synthesis, which will serve to test previous work, including this study, and to provide an evolutionary treatment of a pantropical assemblage of arboreal beetles. We would be pleased to cooperate in making such an endeavor possible.

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Appendix A

[Description of the new species *C. tripunctata* received following completion of MS]

Coptodera tripunctata, new species
Map 20

Type material.-- HOLOTYPE female, labelled: PERU: Loreto, Cocha Shinguito 24May90 74°45'W 05°08'S Erwin de al Colls; TSn/8; insecticidal fogging of *Scheelea* palms with epiphytes at 4 m [USNM].

Type locality.-- Cocha Shinguito, department of Loreto, Peru.

Derivation of specific epithet.-- From Latin *tres* and *punctum*, in allusion to the three discal setigerous punctures on each elytron.

Description.-- Character states of the *C. aerata* group and the following. See Tables III, V and VII for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum rufo-testaceous; elytra piceous; appendages, antennae and mouthparts rufo-testaceous. Ventral surface of head and prothorax rufo-testaceous; mesepisternum, mesepimeron, metepisternum and metepimeron dark brunneous; metasternum darkened slightly laterally; all abdominal sternites dark brunneous laterally, broadly rufo-testaceous medially (elytral epipleuron dark brunneous).

Fixed setae. Disc of elytron with three setigerous punctures.

Elytra. Interneurs impunctate.

Male genitalia. Unknown.

Notes about habitat.-- The type specimen was taken from *Scheelea* palms with epiphytes at 4 m by fogging with an insecticide.

Geographical distribution (Map. 20).-- This species is known only from the type locality in northern Peru.

Chorological affinities.-- The type locality of this species is broadly overlapped by the range of *C. nitidula*.

Phylogenetic relationships.-- The position of this species is unresolved due to the lack of a male specimen.

Material examined.-- Type material only, see above for details.

Appendix B

James K. Liebherr, one of the reviewers of the penultimate draft of the manuscript on which this paper is based, undertook a numerical cladistic analysis of the data in Table XII, using the program Hennig 86, with the mhennig tree finding option. With Dr. Liebherr's written permission and encouragement (in his signed review of the manuscript), and to make our data more readily available to practitioners of current numerical cladistic techniques, we present, as Figs. 41A and 41B the two shortest cladograms that he found. Each of these is 239 steps, which is 12 steps or 5 per cent shorter than the 251 steps of the reconstructed phylogeny illustrated in Fig. 36.

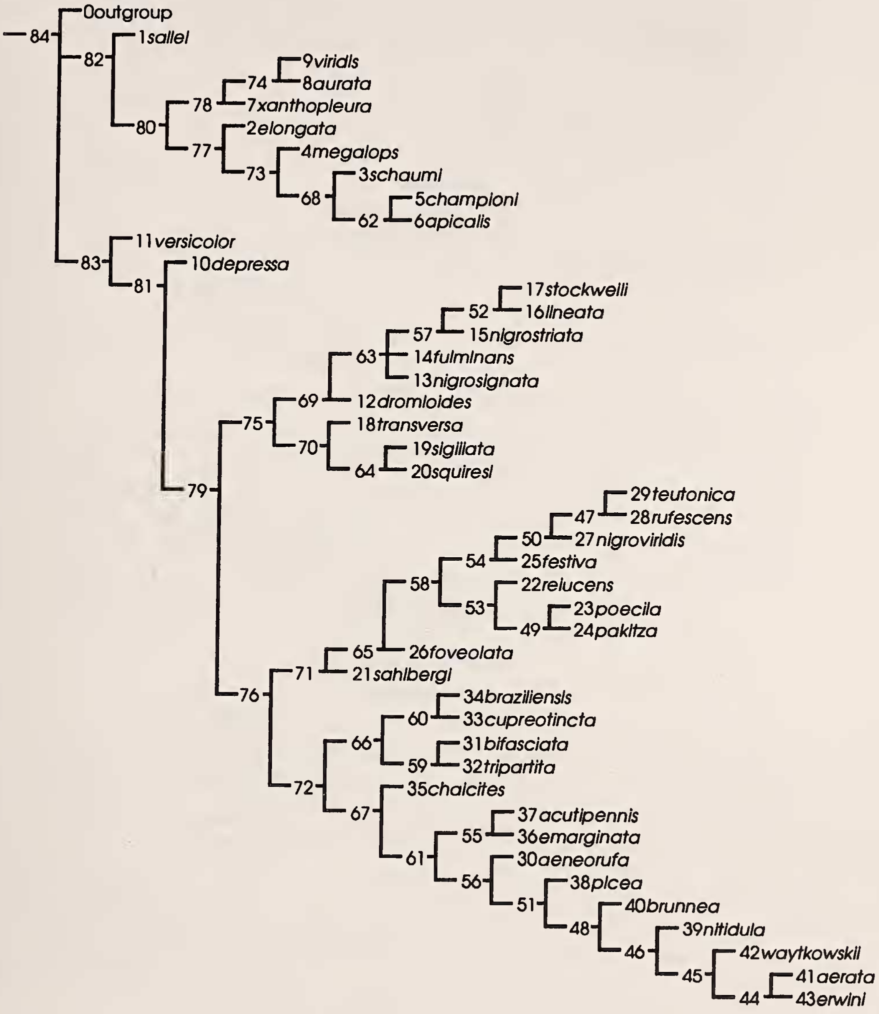

FIGURE 41A,B. The two minimum length cladograms produced by the program Hennig86, mhennig option.

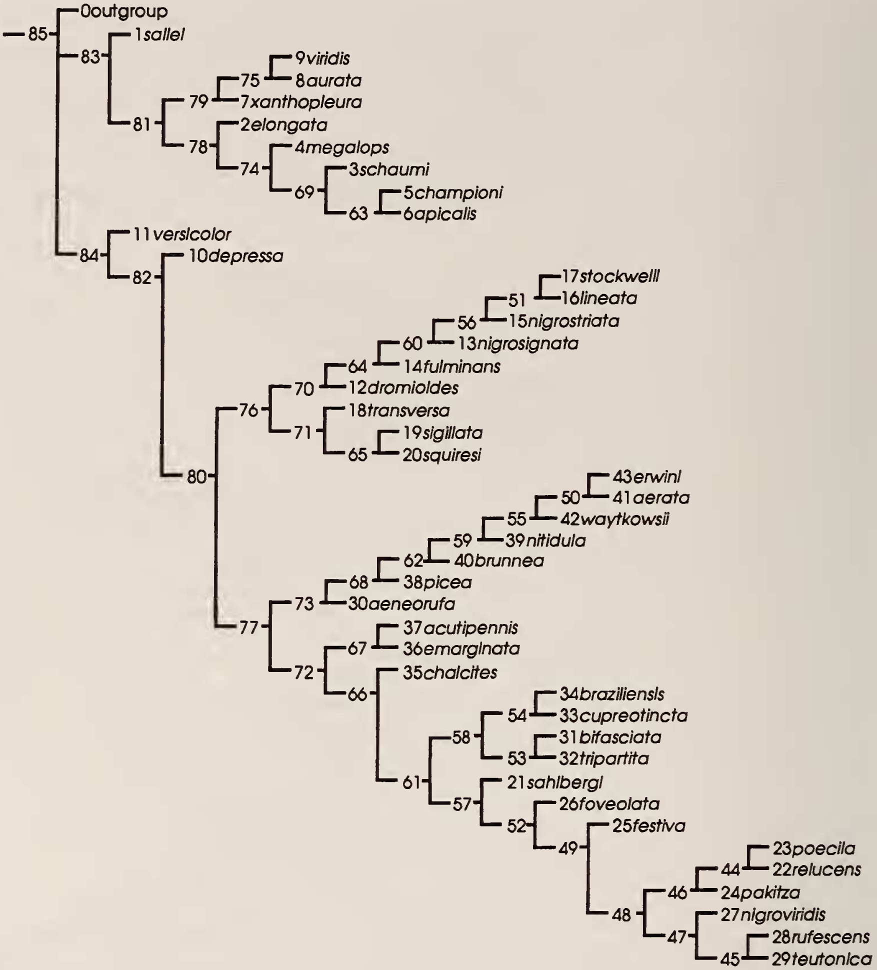

FIGURE 41A, B. - continued.